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THE BEHAVIOR OF ORNITHODOROS ERRATICUS (LUCAS, 1849), SMALL FORM (IXODOIDEA, ARGASIDAE), TOWARDS CERTAIN ENVIRONMENTAL FACTORS[1]

SAMIRA EL-ZIADY[2]

INTRODUCTION

Ornithodoros erraticus (Lucas, 1849) ranges from southwestern Europe through North Africa to Iran. Southwards, small, localized populations occur in Kenya and Uganda. In certain more humid areas, females measure over 5.2 mm. in length; these populations are known as the "large form." In dry areas only the "small form" occurs.

In an initial field study of this tick in Egypt Hoogstraal, Salah, and Kaiser (1954, 1955) found the small form is widely distributed in cultivated and semidesert areas and utilizes a wide range of hosts, especially rodents and hedgehogs, but also burrowing owls, *Varanus* lizards, toads, foxes, and shrews. The present experiments, undertaken in the Medical Zoology laboratories of the United States Naval Medical Research Unit at Cairo, were designed to provide controlled laboratory data for further field studies on the biology, ecology, and epidemiological significance of this species in Egypt.

The large form of *O. erraticus* is well known as the vector of *Borrelia hispanica*, the etiologic agent of Spanish-North African relapsing fever of human beings. The small form is the vector of *B. crocidurae* Leger, 1917 (= *B. microti* Rafyi, 1946, *B. merionesi* Blanc and Maurice, 1948, and *B. dipodilli* Heisch, 1950) (Davis and Hoogstraal 1954, 1955). The large form has also been found infected in nature with Q fever (*Coxiella burnetii*) by Blanc and Bruneau (1955).

METHODS AND MATERIALS

The reactions of *O. erraticus* to five different environmental factors, temperature, humidity, smell, gravity, and light, were tested in two pieces of apparatus substantially similar to those used by Wigglesworth (1941). The first consisted of two copper tanks 20x20x20 cm. held together by a metal strip and separated from each other by an asbestos sheet 5 mm. thick. Hot or cold water circulated in the tanks or, more conveniently, water in the tanks was heated to the desired temperature by means of microburners under the tanks.

Ticks were observed individually in a circular arena placed over the water tanks and thus arranged to offer the experimental subject two different intensities of one factor concurrently. The perforated zinc arena floor was covered by bolting silk (voile). The arena wall, a glass ring 2.5 cm. high and 15 cm. in diameter, was surmounted by a tightly fitting glass cover provided with a central circular hole for introducing ticks; this hole was covered by a microscopic coverslip. Tracks of individual ticks were copied on paper by the observer alongside the apparatus.

In order to eliminate individual bias of single ticks to any single given condition, the two intensities in an experiment were reversed and the same experiment was repeated from five to ten times. Following each experiment, ten ticks similar in respect to feeding condition to the one used were offered the same set of conditions. The number moving to each half of the arena was counted every two minutes, a period found to be sufficient for a moderately active tick to cross one half of the arena. This apparatus was used mainly to test reactions of individual ticks to small differences in any single given factor. It was possible to arrange the two halves in such a way that one half differed from the other with regard to one or more factors simultaneously.

The temperature preference range of both hungry and engorged ticks was tested in the second apparatus, a temperature gradient based on that used by Wigglesworth (1941). This

[1]Accepted for publication January 17, 1957. The opinions and assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

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provided a linear gradation of temperature by applying heat to one end and cooling to the opposite end of a stainless steel trough 50x8x8 cm. Inside this a small inner trough 45x4xl.5 cm. rested on sand saturated with water. Twelve thermometers equally spaced in the sand very close to the inner trough measured its temperature, which was also checked by a thermocouple. The inner trough was covered by a glass plate and the humidity inside was controlled by 80° F. When engorged individuals were required, hungry ticks were allowed to feed on young mice during the night prior to the experiment.

Further details of specialized methods and equipment will be given below.

REACTION OF FEMALE TICKS TO TEMPERATURE

This experiment was designed to determine the influence of temperature on the behavior of female ticks in uniform temperatures and, for

TABLE I

DISTRIBUTION OF 15 ENGORGED FEMALES IN VARIOUS TEMPERATURE ZONES AFTER 15 MINUTES' EXPOSURE

°F.	48–54	54–60	60–66	66–72	72–78	78–84	84–90	100–114
OBSERVATION NUMBER	NUMBER OF TICKS AFTER 15 MINUTES							
1	10	0	0	0	4	0	0	1
2	9	1	0	2	0	3	0	0
3	9	2	0	1	3	0	0	0
4	9	2	0	0	3	1	0	0
5	10	1	1	0	3	0	0	0
6	6	3	0	2	3	0	1	0
7	3	2	6	3	1	0	0	0
8	9	1	2	2	0	0	0	0
Total	65	12	9	10	17	4	1	1

TABLE II

DISTRIBUTION OF 10 HUNGRY FEMALES IN VARIOUS TEMPERATURE ZONES AFTER 15 MINUTES' EXPOSURE

°F.	48–54	54–60	60–66	66–72	72–78	78–84	64–90	90–100	106	116
OBSERVATION NUMBER	NUMBER OF TICKS AFTER 15 MINUTES									
1	7	2	0	1	0	0	0	0	0	0
2	7	1	0	0	0	0	1	0	1	0
3	6	0	0	0	1	0	0	0	3	0
4	4	2	0	4	0	0	0	0	0	0
5	6	0	0	0	1	0	0	0	0	3
6	3			wandering up to 116 F.						
7	8	0	2	0	0	0	0	0	0	0
8	6	1	3	0	0	0	0	0	0	0
9	8	1	0	0	0	0	0	0	0	0
Total	56	10	5	5	2	0	1	0	4	3

covering its floor with a strip of filter paper saturated with the proper salt solution. The linear temperature thus obtained varied from 48° F. at the cool end to 120° F. at the hot end.

Each experiment lasted from fifteen to thirty minutes or longer. However, fifteen minutes were found to be sufficient for the tick to elicit a response to any given factor.

Ticks were brought from the field, separated by sex and developmental stage, and stored in a dark cabinet at a temperature of approximately comparison, in various large and small temperature ranges. Reactions of hungry and of engorged ticks were also compared.

METHODS. *Uniform temperature*: The reactions of engorged female ticks to temperature were first tested in an arena resting on one tank and having a uniform temperature of 70°, 84°, 94°, 104°, or 110° F. Ticks were introduced after humidity and temperature conditions were established in the arena.

Temperature gradients: Fifteen hungry or en-

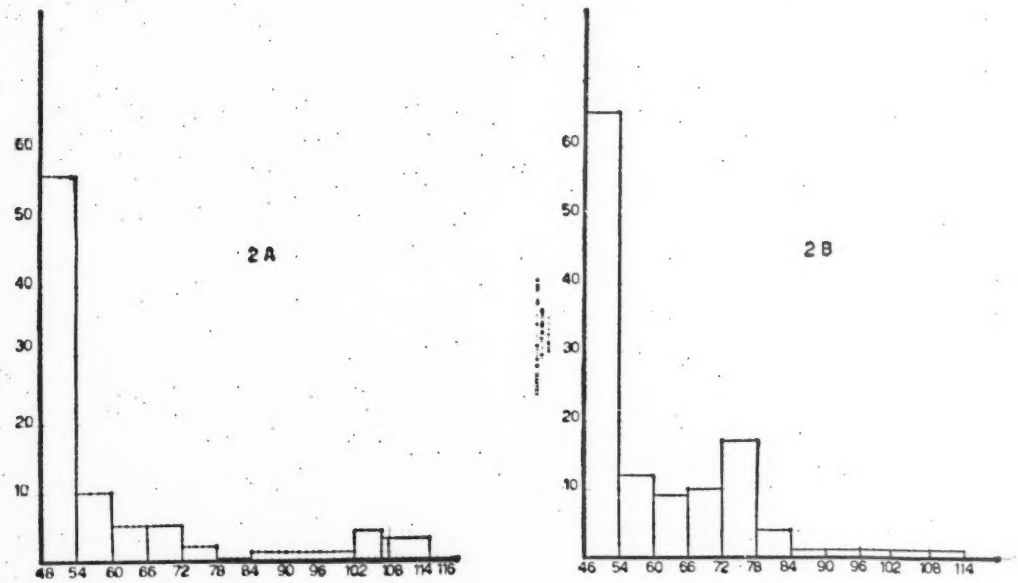
gorged ticks were distributed at random in the inner trough of the apparatus described above. The number against every temperature range was recorded after fifteen minutes had elapsed. The ticks were then redistributed, left for another fifteen minutes, and so on. This was repeated seven or eight times.

Alternative temperatures: The two tanks were brought to the desired temperature by heating or cooling the contained water. The arena in this case rested with one half on one tank and with the other half on the adjacent tank. Temperatures were checked by a thermocouple. The humidity was maintained constant at 75% R.H. by placing four thicknesses of filter paper 2 mm. below the voile floor.

Temperature gradients: Results of these experiments are shown in Tables 1 and 2 and in text figure 2.

In six out of the eight repetitions, nine or ten (i.e. 60% or 70%) of the *engorged* ticks preferred the low temperature range (48°–54° F.) and were found quite close to the coldest part of this range, i.e. at 48° F. Only a single tick in one repetition rested in the range of 82°–87° F. Also, only a single tick was counted in the range 100°–114° F.; this individual wandered up to 120° F. but on approaching this temperature immediately turned back and quickly traveled to the cool end of the temperature range.

When ten *hungry* females were introduced, no definite number remaining in any one temperature



TEXT FIG. 2.—Relative numbers of ticks, hungry (A) and engorged (B), in different temperature gradients after 15 minutes' exposure.

RESULTS. *Uniform temperature*: Figure 1 gives the reactions and the course followed by ticks in uniform temperatures.

Engorged ticks in an arena of 70°, 84°, or 94° F. were very active, moved constantly, and traveled mostly in circles. At high temperatures (104° or 110° F.), on the other hand, the ticks were sluggish and stopped very frequently. When induced to move, the subject usually walked with one side of its body lifted up on the glass wall of the arena (presumably to expose the least surface to contact with the hotter floor). The rate of movement increased with increasing temperature up to 94° F. At higher temperature, 104° or 110° F., the rate of movement considerably decreased and the ticks did not move except after being shaken (Figure 1).

range could be obtained at the end of the fifteen minutes (Table 2), due possibly to the subjects' restless nature when in this condition. However, in the seven repetitions six to eight ticks (i.e. from 66% to 80%) also occurred in the coldest region of the trough (48°–54° F.) similar to engorged females. Three ticks were once recorded settling down in 106° F. In all repetitions, subjects wandered to a temperature as high as 116° F. They usually moved quickly towards the hot region, though on approaching it they immediately returned to the opposite side.

From these experiments it is clearly seen that both engorged and hungry ticks preferred the coldest temperature range (48°–54° F.).

Alternative Temperatures: Engorged females examined under two temperature alternatives

showed two types of behavior. When first offered a relatively wide range of alternatives, such as 70°–94° F., 80°–95° F., 85°–104° F., and 82°–110° F., the subjects decidedly and consistently avoided the warmer side of the arena. When dropped in the centre of the arena, the engorged female almost immediately directed itself to the cooler side. On reaching the separation line between the two halves, the tick stopped, tested the substratum and surrounding air by rapid movements of palpi and forelegs, retreated, and then turned to the cooler side of the arena. This behavior was repeated in each experiment. The intensity of this reaction increased as the temperature difference in the two halves of the arena became greater, as indicated by the tracks in Figure 3.

When engorged ticks were offered relatively narrower alternatives of temperature, such as 75°–84° F. and 80°–90° F., they wandered actively around the arena without evidencing avoidance of the warmer side, as shown by the tracks in Figure 4.

In the first group of temperature alternatives, the difference between the two sides of the arena was 15° F. or more while in the second group the difference in the temperature between the two sides was only 14° F. or less. The results indicate that engorged ticks are indifferent to narrow temperature alternatives (14° F. or less) but that when the difference between the two given temperatures exceeds 14° F., engorged ticks commence to sense and avoid the higher temperature.

Hungry females showed different reactions from engorged females. Tracks of hungry female ticks offered various temperature alternatives are shown in Figure 5. In all combinations offered, one side of the arena was maintained at 80° F., while the other was increased gradually up to 110° F. The temperature combinations were 80°–90° F., 80°–95° F., 80°–110° F., 80°–106° F., and 80°–110° F.

Hungry ticks moved from the cool half to the warmer half of the arena without hesitation even when the warmer side was as high as 106° F. This heat tolerance is in marked contrast to the avoidance of the same temperatures by engorged ticks.

The only indication of sensitivity of the hungry tick to a temperature as high as 106° F. was that it stopped momentarily at the separation line, a behavior not displayed in the other temperature alternatives. Nevertheless, it crossed actively to the warmer half without showing definite turning movements.

Above 106° F., when half the arena offered was 110° F., the tick avoided the warm side and consistently turned back to the cool side when approaching the separation line.

Discussion. From the foregoing experiments, it can be inferred that the reaction of females to temperature depends on whether the tick had taken a fresh blood meal or whether it was hungry.

Hungry female ticks were very agile, restless, and moved continually. While walking they quested in rapid vertical movements, examining the air or testing the substratum with forelegs and palpi. Frequently they took long strides. Engorged females, on the other hand, were relatively sluggish and frequently stopped to quest with the forelegs; on encountering a favorable environment they often folded their legs and remained motionless except when roughly disturbed.

When either engorged or hungry ticks crossed from an apparently favorable half to the other less favorable half of the arena, they usually stopped at the separation line, quested the atmosphere and the substratum, retreated, and then turned back to the favorable half.

Behavior in a temperature gradient also indicates that hungry females are capable of tolerating temperatures up to 106° F. Engorged females, on the other hand, are sensitive to high temperatures inasmuch as they strongly avoided these. They appear to sense a temperature difference above 14° F. but to be indifferent towards two temperatures differing by 14° F. or less. The observed results of differences in sensitivity to temperature between hungry and engorged females may have significant implication in determining the parasite's habitat and geographical range.

Females of another tick species, *Ixodes ricinus*, placed by Lees (1948) in a similar alternative temperature apparatus, crossed from 15°–21° C. (i.e. 59.0° to 69.8° F.) without hesitation but were unable to cross from 15°–27° C. or 34° C. (59.0°–80.6° F. or 93.2° F.) and turned back and walked away. Lees, however, did not mention whether the female ticks he used were fed or unfed.

Reaction of Female Ticks to Humidity

This experiment was designed to gain knowledge concerning the general humidity preference of engorged and hungry female *O. erraticus* and to compare the reactions of individuals in both feeding conditions to changing degrees of humidity in the environment.

Methods. Experiments for testing the responses of female ticks to various relative humidities were conducted in an alternative chamber arrangement described above.

The humidities in the arena were controlled by using saturated salt solutions described by Buxton (1931), and Buxton and Mellanby (1934), and the data from Carr and Harris (1949) recorded by Solomon (1951). The salts were potassium chloride 18%; magnesium chloride 33%; ammonium nitrate 62%; sodium chloride 75%; potassium chloride 83%; calcium phosphate monobasic 95%; potassium sulphate 98%; and water 100%.

These were checked before use by means of a hair hygrometer.

For obtaining a very low humidity, concentrated sulphuric acid (sp. gr. 1.84 and conc. from 95%–98%) was utilized.

In discussing the results it was assumed that in the area of the arena above the voile the humidity was similar to that given by the theoretical values of the salts used and that in the middle line between the two halves of the arena there was a steep gradient. In all humidity studies, temperature was maintained constant at 80° F.

For establishing a humidity gradient, the bottom of the arena was divided into eight sections as represented by Figure 6a and b. Each section was provided with four thicknesses of filter paper saturated with the salt solution and placed approximately 2 mm. below the perforated zinc floor. The relative humidities offered were 18%, 33%, 75%, 95%, 98%, and 100%.

In alternative humidity studies, the tick was first offered two humidity extremes, one very low and the other very high. For this purpose, a petri dish approximately 15 cm. in diameter was divided into two sections by a glass partition.

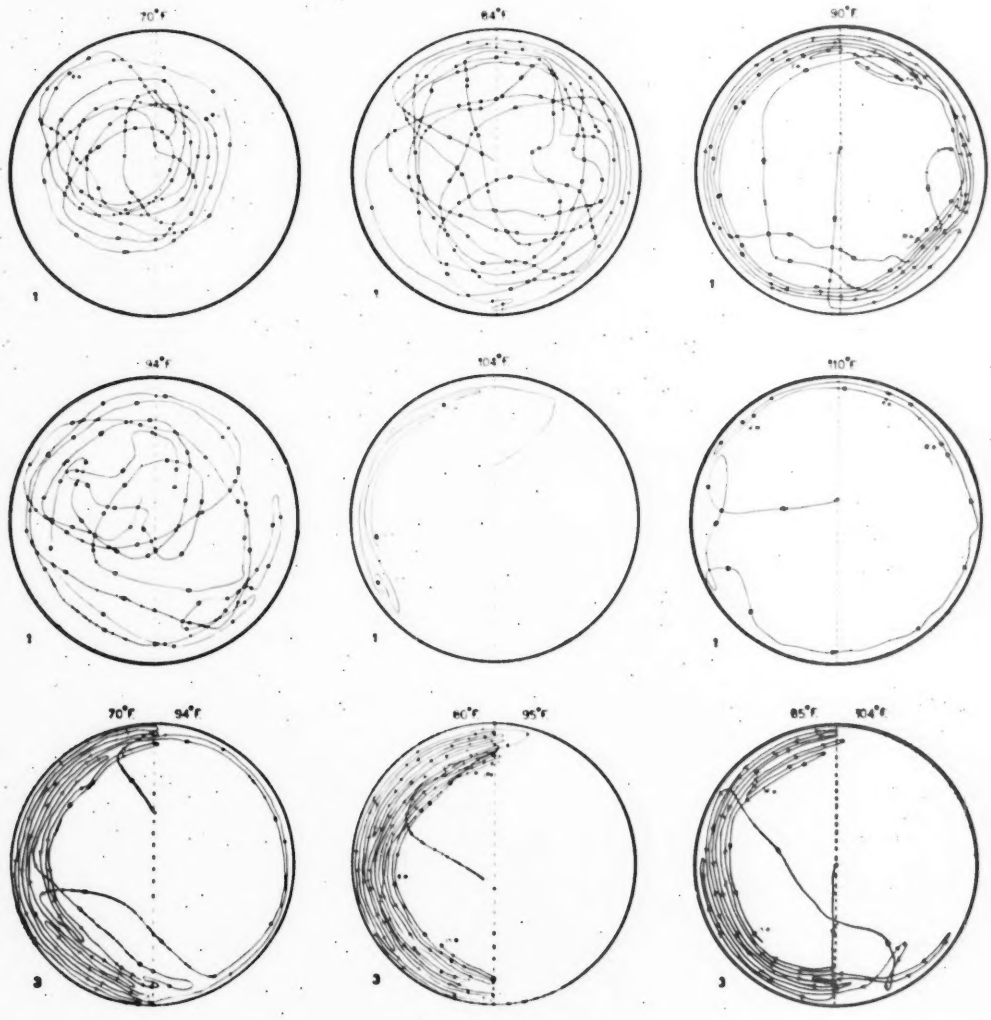


PLATE I

1. Reactions of engorged females in uniform temperatures; 2. Reactions of engorged females to alternative temperatures.

In one, concentrated sulphuric acid provided very low humidity (dry side), while in the other water gave saturation (wet side). The arena was placed above this arrangement as usual.

RESULTS. *Humidity gradients*: When *engorged females* were offered various humidity ranges, they responded by tracks (Figure 6a), indicating their preference for regions of low and medium humidities, 18%–33% and 75% R.H. When approaching the line separating these from relatively high humidities (95%, 98% and 100% R.H.), subjects retreated, turned about, and exhibited usual avoiding reactions. Sometimes, however, they proceeded into the wetter side (95% area) but they usually traveled only a short distance before returning to the lower humidity area (Figure 6a).

When *hungry ticks* were offered the same arrangement, they behaved differently (Figure 6b), showing marked preference for higher rather than for lower or medium humidities. In an arena with the above set of conditions, they avoid the low and medium humidities (18%, 33%, and 75% R.H.) and restricted their activity and wandering to the area of high humidities (95%, 98%, and 100% R.H.). When hungry females crossed to the area of 75% or 18% R.H., they

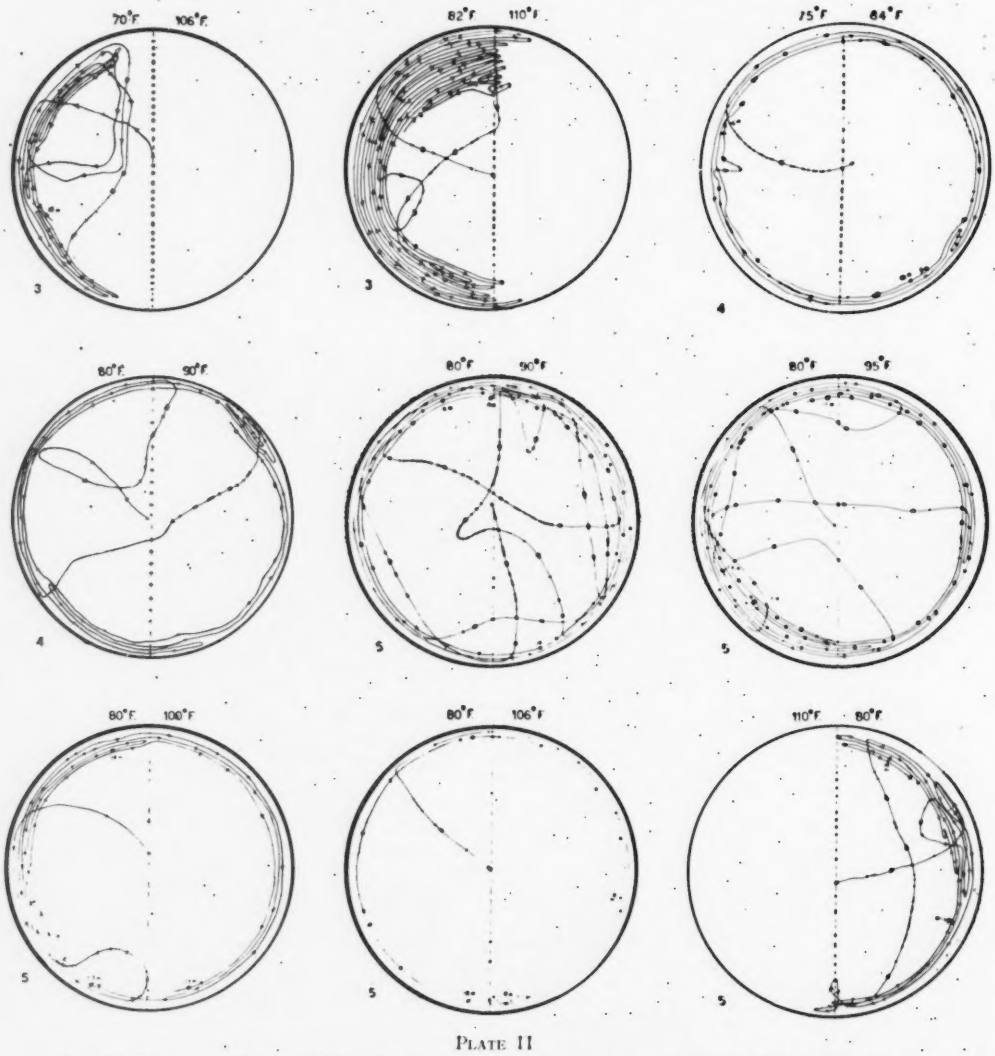


PLATE II

3 and 4, Reactions of engorged females to alternative temperatures; 5, Tracks followed by hungry females in various alternative temperature combinations.

soon turned back to the wetter side of the arena (Figure 6b).

Alternative humidities: The behavior of ticks towards various humidities was further tested in the alternative chamber, where two extremes of humidity were provided simultaneously.

Reactions of an *engorged female* to extreme humidity combinations are shown in Figure 7a. The tick crossed indifferently from the wet side to the dry side of the arena and vice versa without avoiding either, but was extremely sluggish in both sides. It hesitated at the midline and frequently turned without completing a full round of the arena. It mostly stood fast, retracted its appendages, and did not move unless disturbed. Another type of reaction (Figure 7b) shows undirected movements, frequent turning, and sluggishness.

On the other hand, *unfed females* showed marked and strong avoidance of the dry side of the arena and constantly remained on the wet side (Figure 7c). When approaching the steep gradient of the midline, the subject always retreated and turned back to the wet side.

The following relative humidity combinations were then offered to engorged females: 98%–18%.

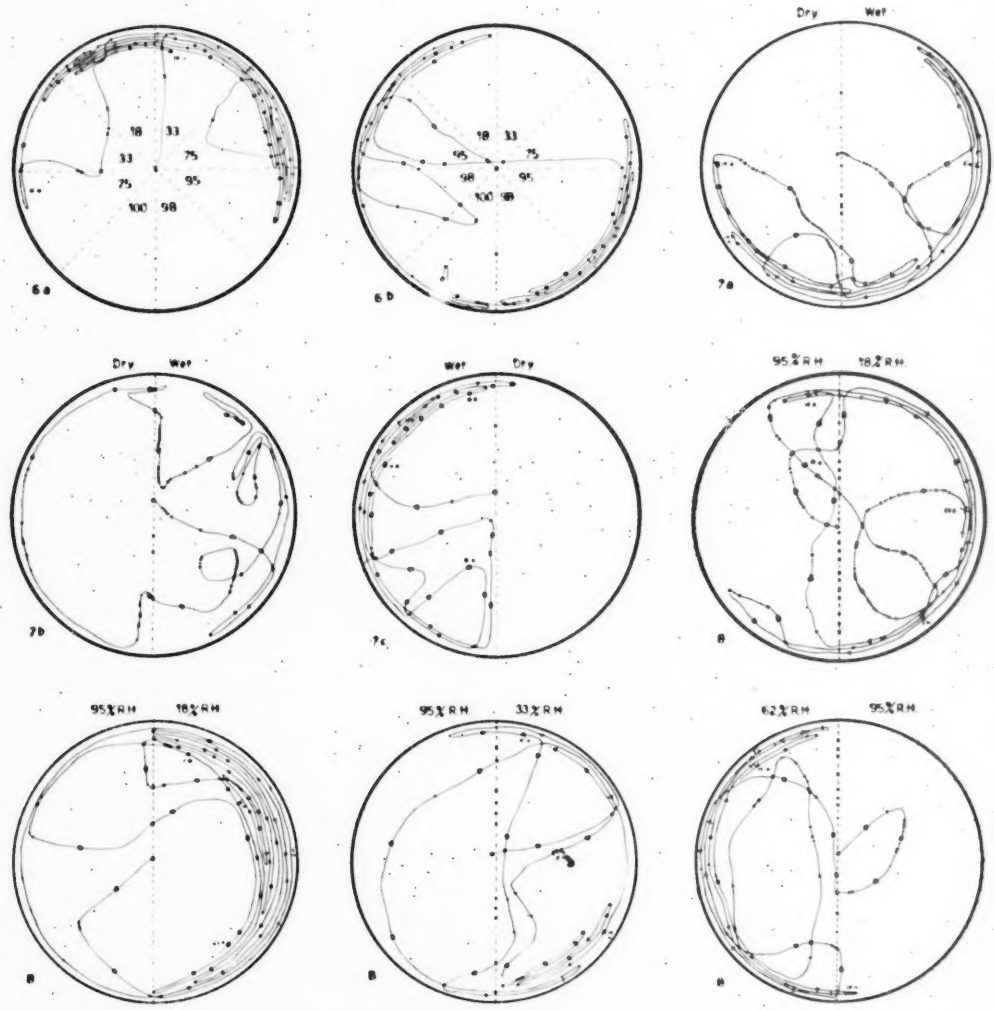


PLATE III

6. Tracks of single engorged (a) and hungry (b) females in an arena divided into sections with different humidities; 7. Tracks of engorged (a and b) and hungry (c) females offered two extremes of humidity; 8. Tracks of engorged females in various combinations of high, low, and medium humidities.

95%–18%, 95%–33%, 95%–62%, 95%–75%, 95%–83%, 95%–98%, and 95%–100% R.H.

In all these combinations, with the exception of the last three, the engorged ticks almost always showed a consistent avoiding reaction to the side of high humidity, i.e. 95% R.H., and were most active in the drier side of the arena (Figure 8).

An engorged tick dropped on the middle line of the arena immediately crossed to the dry side. When reaching the middle line from the low humidity side it stopped hesitantly testing the environment and usually retreated and turned back to the dry side. If it happened to cross the humid side of the arena, it usually increased its rate of movement till it returned to the side of the lower humidity. This reaction was constantly demonstrated in all relative humidity combinations.

In the last three humidity combinations, i.e. 95%–83%, 95%–98% and 95%–100% R.H., however, the engorged tick showed no preference for either combination and wandered from one half of the arena to the other without hesitation. However, its rate of movement was very much slower in comparison to that in medium and relatively low humidities.

When the engorged tick was given sets of

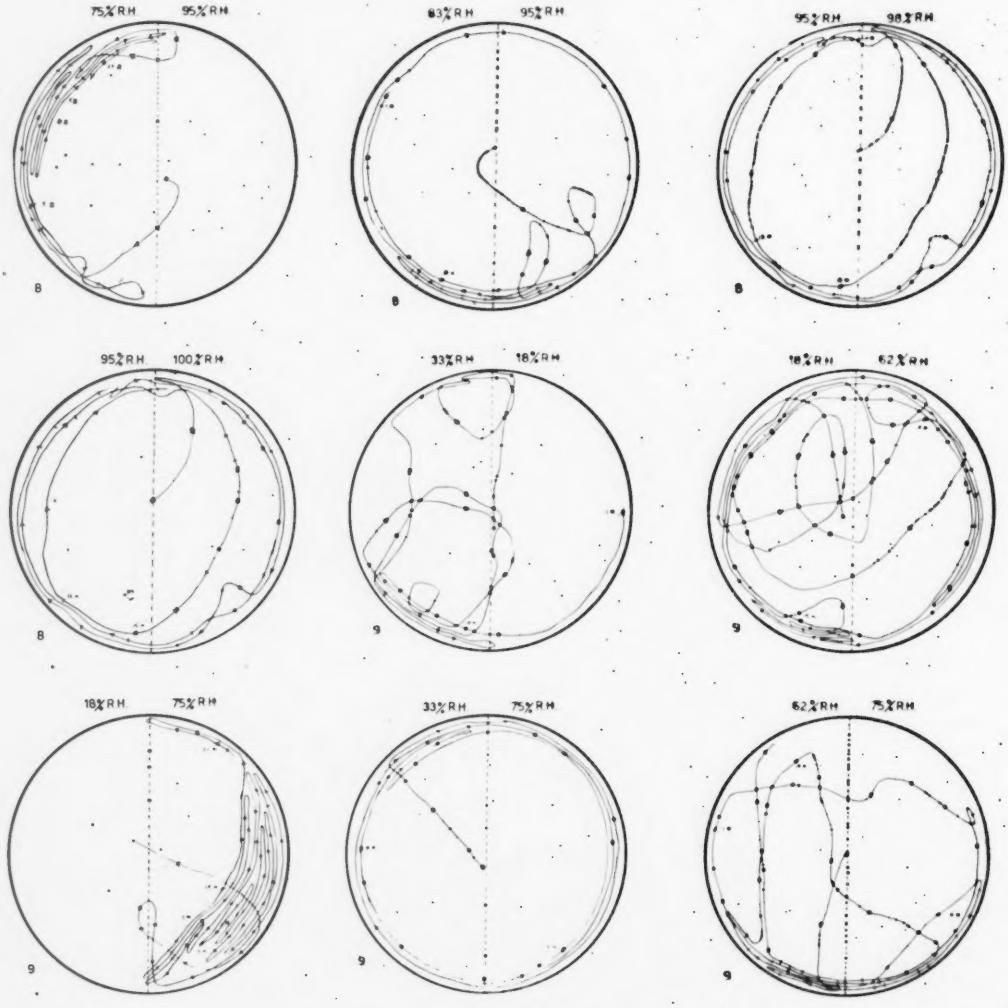


PLATE IV

8, Tracks of engorged females in various combinations of high, low, and medium humidities; 9, Reactions of engorged females in various combinations of low and medium humidities.

medium and low humidity combinations, such as 18%–33%, 18%–62%, 18%–75%, 33%–75%, and 62%–75% R.H., it always preferred the wetter side of the arena to the drier side (Figure 9). In combinations of 33%–75% and 62%–75%, however, these subjects were quite indifferent and crossed unhesitantly from the drier to the wetter side, although with slightly increased preference for 75% R.H. (Figure 9).

Unfed or hungry ticks, on the other hand, gave a markedly different response. Offered humidity combinations of 95%–83%, 95%–75%, 95%–62%, 95%–33%, and 95%–18%, they strongly and consistently avoided the side of lower humidity and immediately turned back into the wet side when reaching the middle line (Figure 10). The hungry tick also avoided a relatively high humidity as 83% in a combination of 95%–83%. But when the hungry tick was given a combination of 95% and 100% R.H. it crossed freely from one side to the other without hesitation (Figure 10).

REACTION OF PRECONDITIONED FEMALE TICKS TO HUMIDITY

Humidity conditions in which fed or unfed female *O. erraticus* were previously exposed may

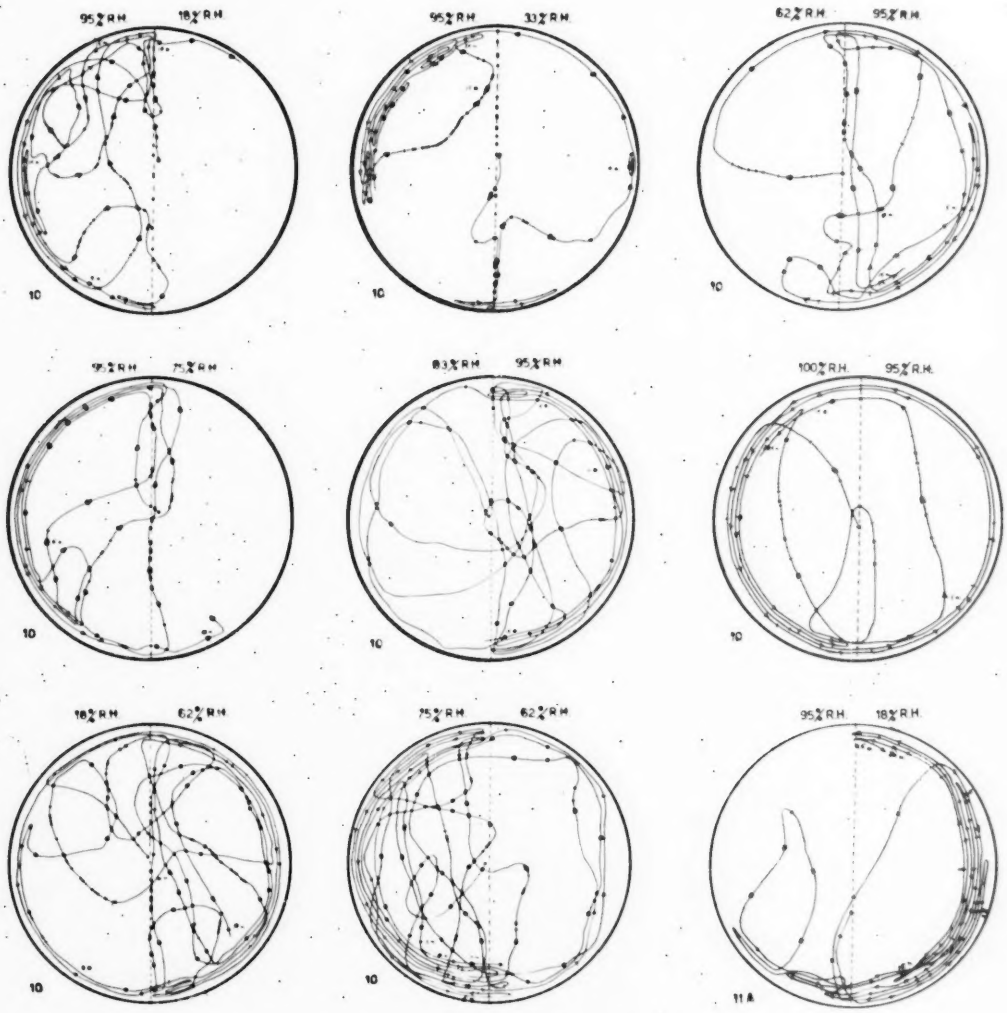


PLATE V

10. Tracks of unfed females in various humidity alternatives; 11A, Reactions of engorged females, preconditioned at 95% R.H., to alternatives of 18% and 95% R.H.

have exerted a significant influence on their response to various humidities during the experiments described above.

The characteristic water balance in the body of each species of tick, especially when unfed, can be maintained by absorption or loss of water through the body surface, as shown by Lees (1946) for *I. ricinus*, a species whose optimum area when unfed is 95% R.H. The reactions of individuals of each species, therefore, vary as they seek to maintain their normal water balance and may depend on an attempt to recover from unfavorable exposure.

The following tests were designed to determine whether conditions in which engorged or unfed ticks had been exposed exerted a significant influence on their response to various humidities.

METHODS. Engorged and hungry females from laboratory stock that had been maintained under fluctuating conditions of relative humidity were held for varying periods (the lowest four hours and the highest 36 hours) over either 95% R.H. or 18% R.H. (these will be referred to as wet and desiccated ticks respectively). These preconditioned ticks were then offered the choice of 95% or 18% R.H. in the alternative chamber.

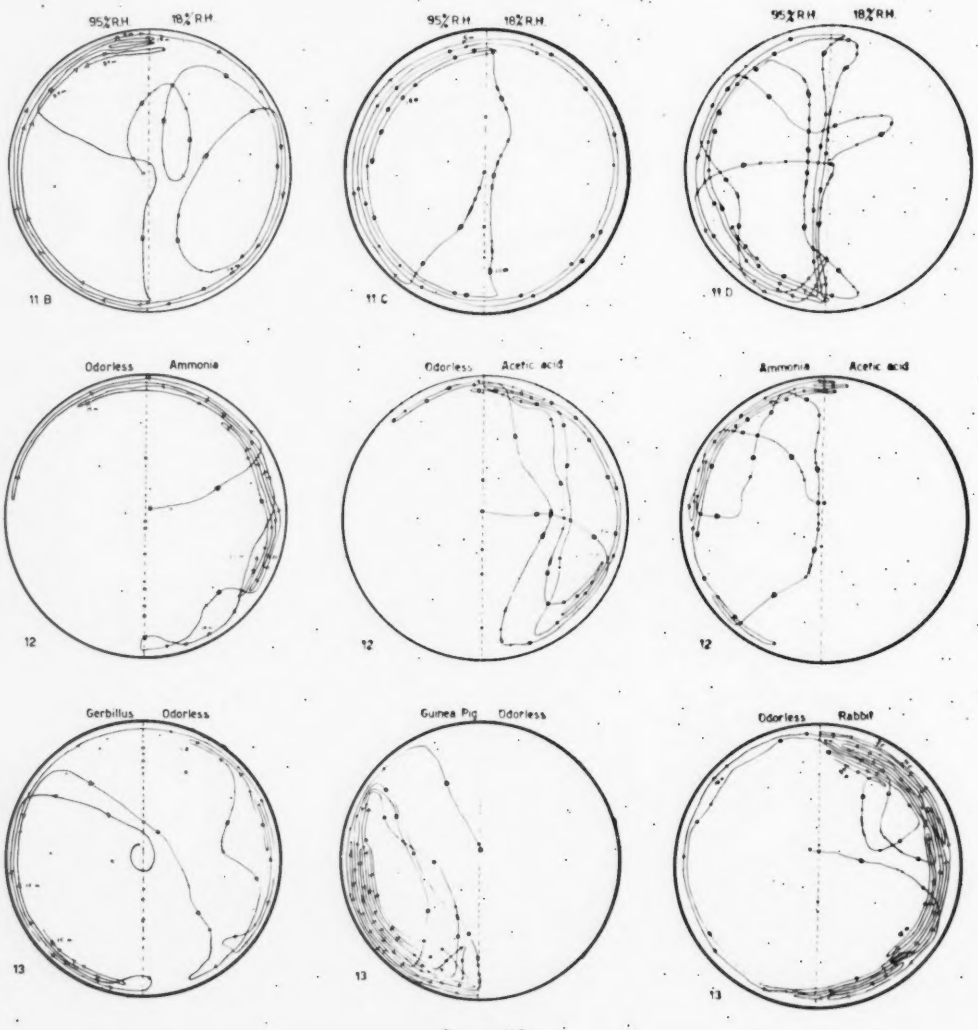


PLATE VI

11B, Reactions of engorged females, preconditioned at 18% R.H., to alternatives of 18% and 95% R.H.; 11C, Same, with hungry females preconditioned at 95% R.H.; 11D, Same, with hungry females preconditioned at 18% R.H.; 12, Reactions of hungry females to odors of ammonia and acetic acid; 13, Reactions of hungry females to odors of various mammals.

RESULTS. All subjects, whether hungry or engorged or whether preconditioned for a long or a short period, behaved in the same manner towards the humidity combinations.

Figure 11A shows the reaction of *wet, engorged* females in the alternative chamber with the humidity combination 95%–18% R.H. The tracks indicate that wet engorged ticks (preconditioned over 95%) preferred the dry side of the arena (18% R.H.) to the wet side (95% R.H.). This avoidance was not manifested as soon as the tick was dropped in the arena but occurred after about a minute.

When desiccated, *engorged* females (preconditioned on 18% R.H.) were offered these combinations, the reaction was reversed and the ticks avoided the lower and chose the higher humidity. They also took some time to discriminate the difference in humidity.

Desiccated, *hungry* ticks offered the same conditions, immediately and consistently avoided and turned back from the low humidity side (18%) when approaching the middle line. Wet hungry ticks crossed from the wet to the dry side without hesitation, but after a time they began to avoid the dry side (Figure 11C & D).

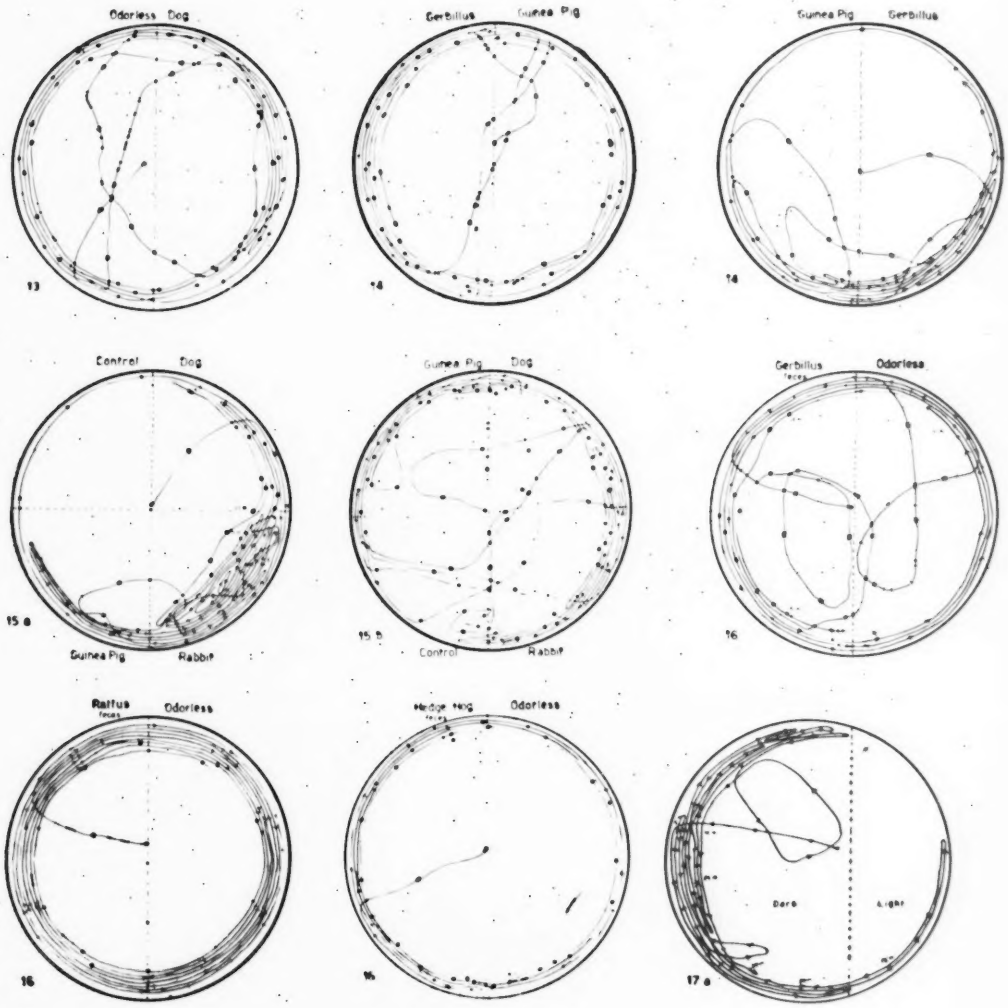


PLATE VII

13, Reactions of hungry females to odors of various mammals (continued); 14, Tracks of a hungry female in an arena with *Gerbillus p. pyramidum* and guinea pig as alternative hosts; 15, Reactions of hungry female (a) and hungry male (b) to odors of various mammals; 16, Reactions of hungry females to animal feces; 17a, Reaction to horizontal light range.

DISCUSSION. Results of the above experiments indicate that while engorged ticks strongly avoid low and very high humidities and prefer medium humidities, hungry ticks, on the contrary, strongly avoid low or medium humidities and are much more active in high humidities.

Optimum humidity for engorged ticks appears to be within the range of 62%–75% R.H. and for hungry ticks 95% R.H.

However, humidity responses of ticks depend on their previous physiological state, particularly on their water balance. These responses are not merely a preference for one set of humidity conditions.

Readiness of desiccated unfed ticks to rest in moist air may be ascribed to their ability to gain water in order to attain their normal balance; desiccated ticks are therefore more sensitive to this factor than engorged ticks, which attain their water balance through blood sucked from their host (Lees 1946).

Ixodes ricinus, as shown by Lees (1948), behaved in a fashion similar to *O. erraticus* in that if its water content was normal, it avoided high humidities and moved with equal readiness in dry or moist air. "After desiccation, however, the ticks were readily arrested in moist air" (Lees 1948).

Krijgsman (1937) observed that while young *Boophilus* larvae were indifferent to humidity, older larvae aggregated near wet cotton wool. Howell (1940) found that unfed nymphs and replete females of *Dermacentor albipictus* placed in a linear gradient eventually came to rest at a humidity higher than 70%, mostly at 85% R.H.

SEARCHING BEHAVIOR OF FEMALE TICKS

Searching for a host, *O. erraticus* usually travels at random. These experiments were undertaken to determine whether host seeking is a kinetic or a tactic reaction.

METHODS. A young, hairless mouse was put at one end of a small cardboard box approximately 8" x 5" x 4". A number of hungry ticks were introduced at the other end of this box.

RESULTS. Ticks introduced into the box with the mouse wandered in all directions and distributed themselves around the box. When finally approaching the mouse, they failed to detect its presence. However, when they came in actual contact with the mouse they first felt it with the forelegs, probed, and then immediately inserted their mouthparts and started engorging. Some ticks, however, climbed on the animal, feeling with the forelegs and mouthparts as they moved along, and then inserted their mouthparts and started sucking.

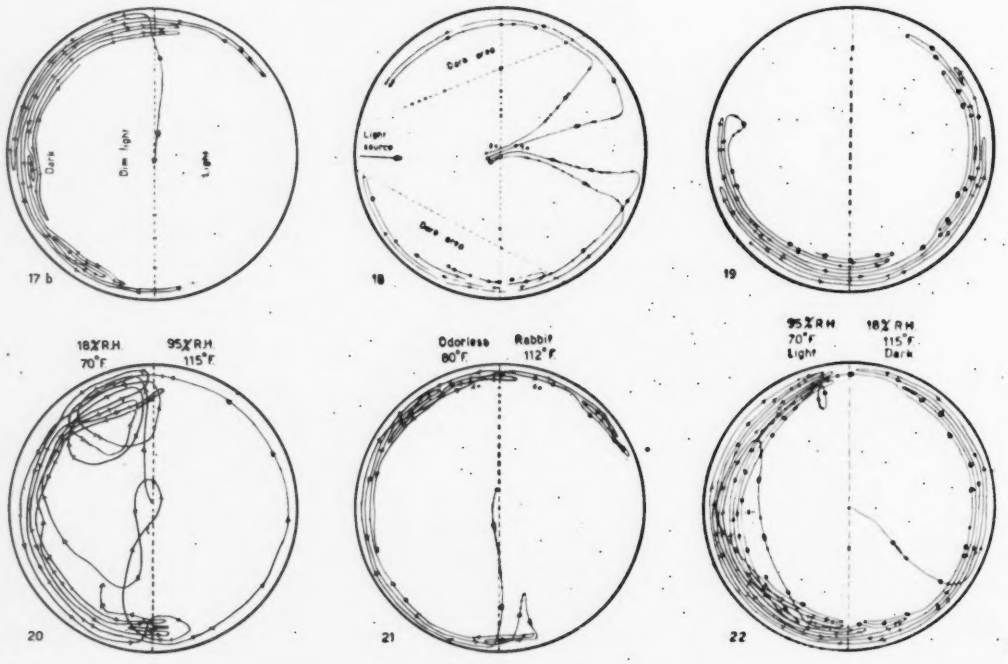


PLATE VIII

17b, Reaction to horizontal light range (continued); 18, Reactions to a divergent horizontal beam of light; 19, Reactions to an overhead light; 20, Reactions to alternative combinations of temperature and humidity; 21, Reactions of hungry female to alternative combinations of temperature and odor; 22, Reactions of females to alternative combinations of temperature, humidity, and light.

In another experiment, a young mouse was placed in a small jar with a number of hungry ticks. They also seemed unable to detect the presence of the host except when coming in actual contact with it.

No preference for a particular part of the host's body was indicated by feeding ticks. Offered a hairless young mouse, the ticks attached to any part of the host's body that they encountered, such as tips of toes, snout, and even the tips of the nose or the tail.

It appeared probable that the hair of the adult host hindered the tick during attempts to engorge. A newly cut hairy tail was offered with another hairless one. On the former, the tick was indifferent and did not even attempt to probe, but on the latter the same tick felt the tail, probed, and inserted its mouthparts to suck blood.

The tick was unable to attach to the palm of a human hand, probably because of the tough skin, and soon moved to the back of the hand where it attached and commenced engorging.

DISCUSSION: See Discussion under next section.

REACTION OF FEMALE TICKS TO ODORS

This experiment was designed to determine whether odors from the animal body, hair, or feces, or any odoriferous chemical in the feces, attracts *O. erraticus*.

METHODS. The behavior of hungry ticks in the presence of various odors was analyzed in the alternative chamber by use of acetic acid, ammonia, hair of various mammals, and rat feces.

In these experiments, the material was disposed 2 mm. below one half of the zinc floor while the other half remained neutral, i.e. free of any odor.

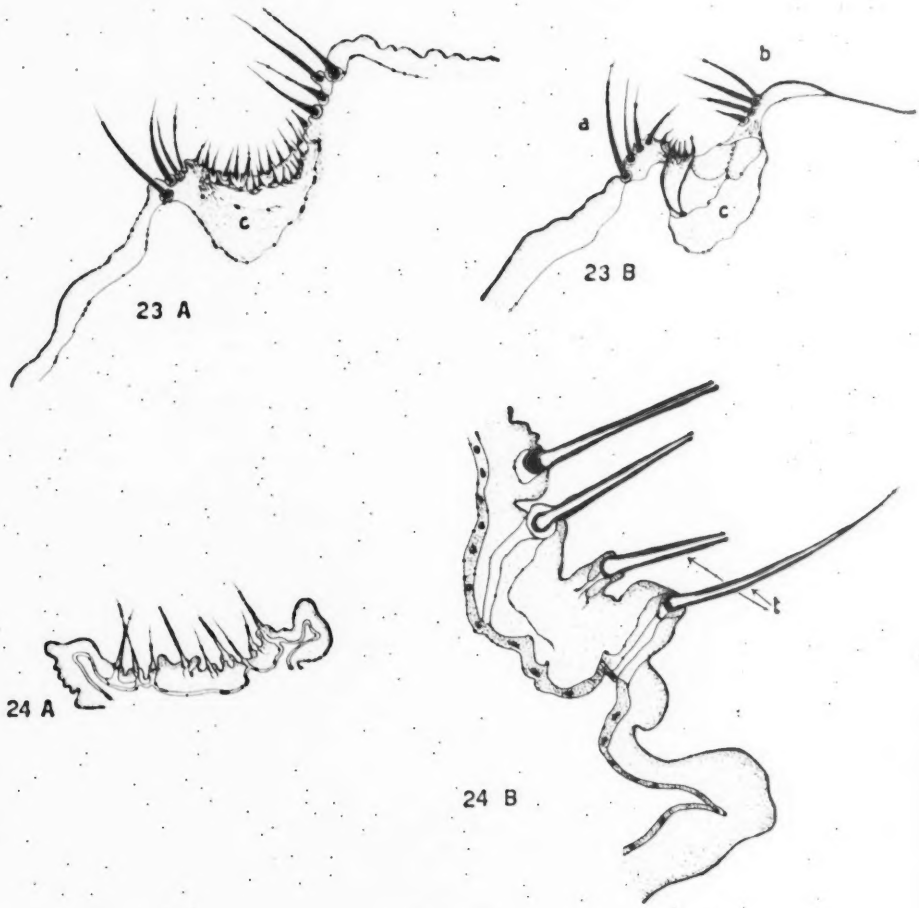


PLATE IX

23, Haller's organ in anterior view (A) and posterior view (B). a, proximal group of bristles; b, distal group of bristles; c, depression. 24, A and B, Transverse section of mouth hood.

The acetic acid and ammonia were used at a concentration of 1.0% and 0.5%, respectively. Hair was freshly cut from the Egyptian gerbil (*Gerbillus p. pyramidum*), guinea pig, rabbit and dog. The feces tested were those of *Rattus rattus*, *Gerbillus p. pyramidum*, and hedgehog (*Hemiechinus auritus aegyptius*). The feces were thoroughly ground, mixed with water, filtered, and the filtrate was used. Temperature and humidity were kept constant at 90° F. and 95% R.H., respectively.

RESULTS. When one half of the arena offered to the hungry tick was scented with ammonia or acetic acid and the other half remained neutral, the tick usually avoided the non-scented side (Figure 12). When one side offered to the tick was ammonia and the other side acetic acid, the tick avoided the acetic acid, preferring the ammonia-scented side, where it remained (Figure 12).

As it went along the scented side, the tick usually felt the surface with the palps and probed through the voile floor. It also lingered on the scented side for longer periods than on the odorless side.

Figure 13 shows the reactions of hungry ticks to odors of different animals. Offered hair of *Gerbillus p. pyramidum*, the subject apparently sensed the difference between the scented and the odorless side. It did not avoid the odorless side but traversed it much more quickly than the other half, in which it stopped very frequently and probed through the voile floor of the arena.

Sometimes, after wandering for a while, the tick stopped completely in the scented side and immersed its mouthparts through the voile into the hair below. Even if disturbed, it returned to this activity.

When provided hair of a guinea pig as a source of odor, the hungry tick strongly avoided the odorless side. This reaction was so intense that the tick usually turned back when approaching the middle line. It is of interest that the scent from guinea pig hair was stronger to the human nose than that of *Gerbillus p. pyramidum*. Similar behavior was exhibited by the tick when rabbit hair was provided, as it consistently avoided the odorless side.

Offered dog's hair in one side of the arena while the other remained neutral, the tick crossed freely from one side to the other without hesitation. The only indication of sensitivity to this odor was that the tick stopped more frequently in the scented half and probed with the mouthparts.

When the two halves of the arena contained different animal scents, the tracks in Figure 14 were obtained. With *Gerbillus* and guinea pig offered as alternatives to the hungry tick, the *Gerbillus* was preferred to the guinea pig. The latter was not avoided, but slight attraction to the *Gerbillus* side was shown by some turning reactions from the guinea pig to the *Gerbillus* side.

When the hungry tick was given four scents, guinea pig, rabbit, dog and nothing (control), each in a separate quarter of the arena, it was sensitive to the rabbit rather than to the dog or the guinea pig (Figure 15a).

A hungry male, for comparison, when offered the same set of odors showed equal preference to all three scents and avoided the odorless side. Testing with the forelegs and the probing with the mouthparts occurred during the entire period of observation (Figure 15b).

Reactions to feces of animals that serve as hosts for *O. erraticus* and that occur in its normal environment were also examined. In this case, filter paper soaked in filtrate of the feces was used or, more conveniently, feces were placed in voile below the zinc floor. Feces tested were those of *Gerbillus p. pyramidum*, *Rattus rattus* and hedgehog (*Hemiechinus auritus aegyptius*). One half of the arena was provided with this material and the other remained neutral. The tracks (Figure 16) resulting from these tests indicate that the tick crossed freely from the scented to the odorless half, showing indifference to feces odor. With *Gerbillus* feces, however, the tick showed some slight tendency to move to the scented side and probed through the voile; this slight tendency, however, did not appear to be significant.

DISCUSSION. From the above results, we may speculate that the hungry tick searches for its host at random, unable to detect it from a distance and becoming aware of its presence only when coming in actual contact with it. But the tick is able to recognize an area contaminated with the host's scent and distinguishes it from an area free of scent.

For feeding, the experiments also indicate that the host's hair is a hindrance to the tick when engorging and that the parasite prefers hairless parts of the host's body. When hairless parts are not available or not within its reach, the tick does engorge from slightly hairy parts of the body. Certain hosts also seemed to be more attractive to the tick than others.

Krijgsman (1937) found that *Boophilus* larvae can distinguish different hosts by smell and that the scent of cow or horse is preferred to that of man.

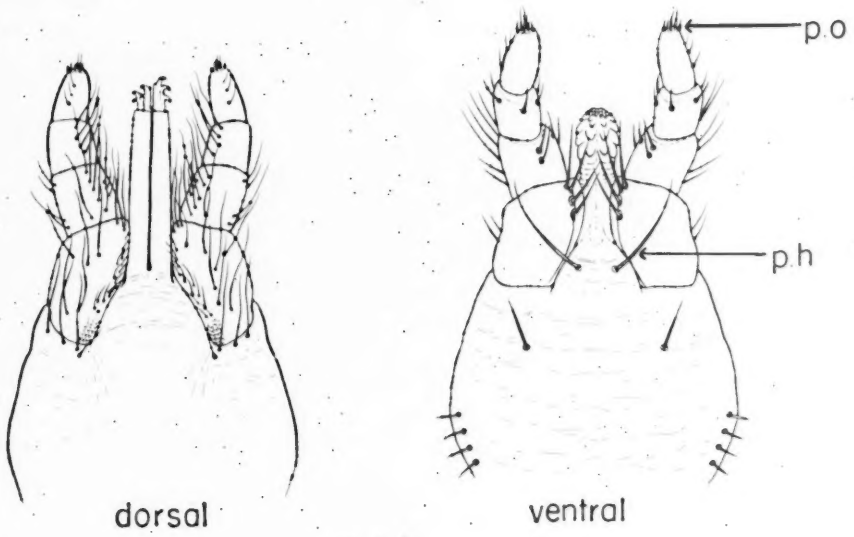
Lees (1948), on the other hand, observed that hungry *Ixodes ricinus* were attracted to sheep's wool only when the temperature of the wool was 37° C. or over.

REACTIONS OF FEMALE TICKS TO GRAVITY

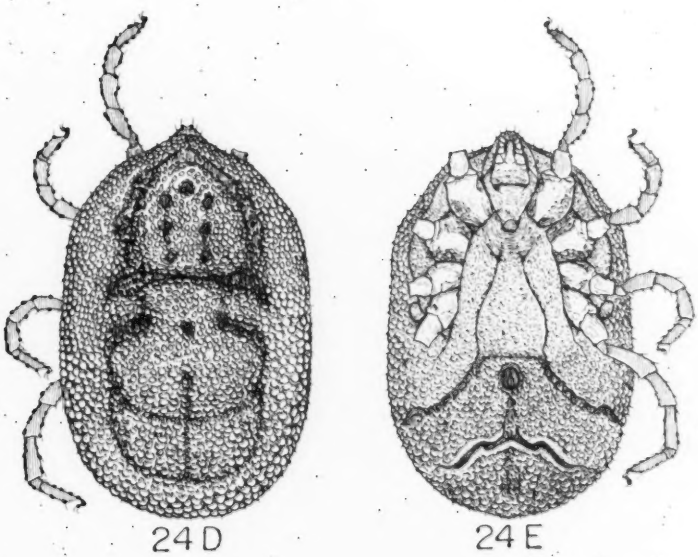
The effect of gravity on both hungry and engorged females was tested in order to determine its influence on their wandering capacity.

EXPLANATION OF PLATE X

PLATE X.—24C, Capitulum; p. o., palpal organ; p. h., posthypostomal bristles (all bristles figured are tactile). 24D, Male, dorsal view; 24E, Male, ventral view; 24F, Male, lateral view.

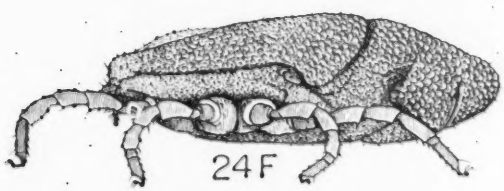


24C



24D

24E



24F

METHODS. Gravity responses of adult females were tested in a glass tube 2 cm. in diameter and 50 cm. long. The tube was lined inside by a strip of filter paper slightly wetted with a suitable salt solution in order to control the inside humidity and to provide a somewhat rough surface for the ticks to walk on. Room temperature, approximately 82° F., was used. The vertical tube, corked at both ends, was held by a clamp and shielded from direct light.

RESULTS. Ten hungry females introduced to the bottom of the tube immediately climbed upwards and wandered for a while around the top, where they finally stopped and clung to the cork.

When the tube was inverted so that the resting ticks were at the bottom of the tube, they began to quest, became aroused, and started climbing to the top of the tube.

When engorged ticks were tested in the same manner they at first exhibited a negative geotactism and wandered up the tube. Very few reached the top of the tube and most soon climbed down

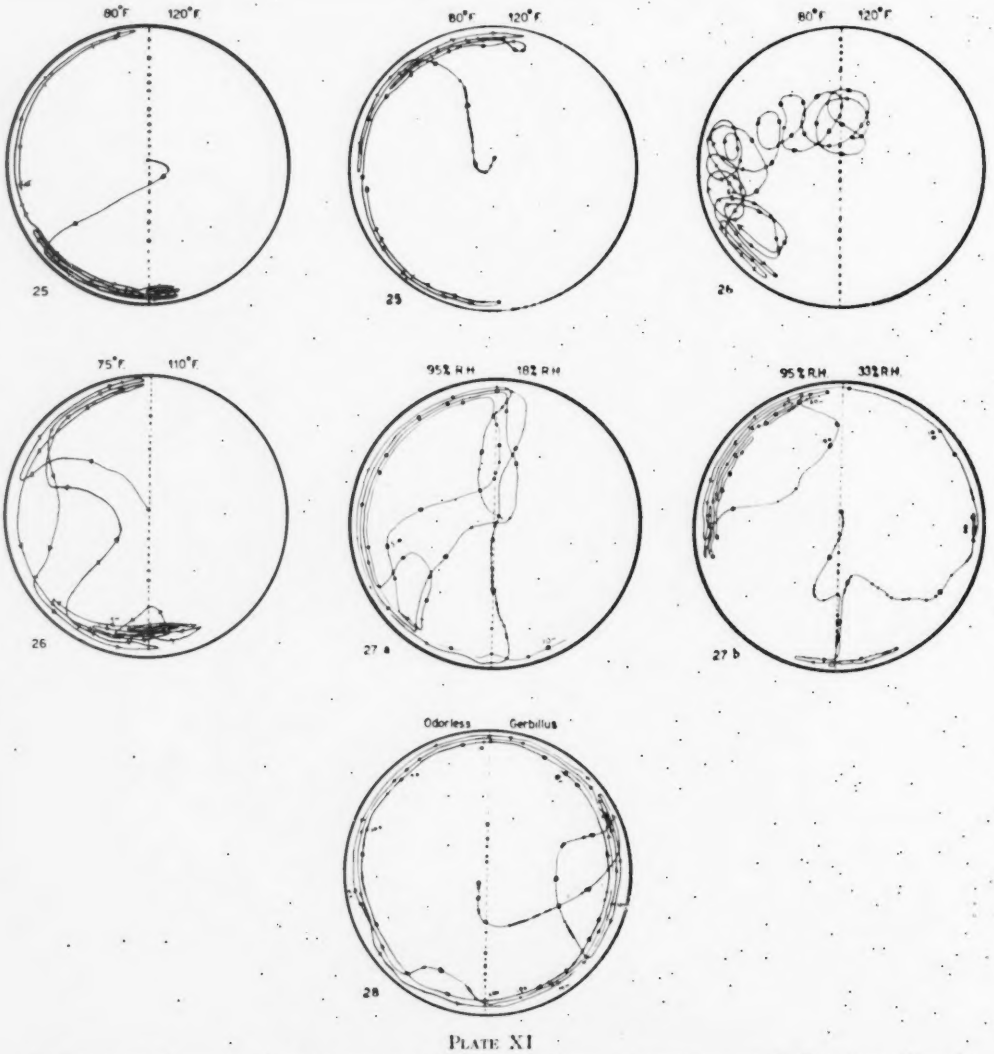


PLATE XI

25, Reactions of hungry ticks with amputated fore tarsi to alternative temperatures; 26, Reactions of females with vaselined mouthparts, hood, and palpi to alternative temperatures; 27, Reactions to alternative humidities of females with (a) amputated fore tarsi and (b) vaselined mouthparts, hood, and palpi; 28, Reactions of hungry ticks with amputated fore tarsi to odors.

again and congregated at the bottom of the tube.

When the filter paper lining the tube was folded at various distances from both ends so as to provide suitable hiding places, hungry ticks usually hid in the upper fold while engorged ticks rested in the fold near the bottom.

When engorged ticks were forced to climb up by strongly illuminating the bottom end of the tube (this factor, as will be mentioned later, was avoided by the ticks), the subjects came to the nearest fold away from this new stimulus and aggregated there with their anterior end in immediate contact with the darkest area of the fold.

When hungry ticks were forced to climb down by illuminating the top of the tube, they climbed downwards but rested in the darkest end near the top.

Discussion. From these reactions it can be said that hungry ticks are generally negatively geotactic and engorged ticks are positively geotactic. That the reactions of subjects in the latter feeding state are not due to their heavy body weight is indicated by the demonstrated ability of engorged *O. erraticus* to climb up the tube if forced to do so.

O. erraticus is a subterranean tick and its gravitational response may depend only on its feeding condition. When ticks were satisfied nutritionally they exhibited almost no tendency to wander. Hungry ticks, on the other hand, always wandered about; their negative geotactism may well be within the scope of searching for the host wherever it lies anywhere in the burrow, sometimes in an upward direction.

When covered by approximately two inches of dry sand, hungry female *O. erraticus* are capable of making their way through the covering layer to the upper surface.

From the available literature it appears that reactions of other species of ticks to gravity depend on the method by which they secure their host. *Ixodes ricinus*, which is in the habit of climbing up vegetation and waiting for a passing host, exhibits negative geotaxis of a tactile nature (Lees, 1948). The same species was found by MacLeod (1935) to be negatively geotactic only within a certain range of temperature, 14° to 24°C.; otherwise it was positively geotactic. *Boophilus annulatus* usually distributed itself randomly and was apparently unaffected by gravity (Krijgsman, 1937).

Reaction of female ticks to light

Since *O. erraticus* possesses no eyes its photic responses were observed in order to determine its sensitivity to this factor.

Methods. The arena was arranged as usual and a horizontal beam of light from a 60 watt microscope lamp was directed to it in a manner to allow one half to be illuminated and the other half to be kept completely or almost completely dark. In another arrangement the horizontal beam of light was directed to the middle of the arena as a divergent cone with its highest light intensity in the middle and with the periphery of the arena dark. The temperature and humidity of the arena were uniform, at 90° F. and 75% R.H.

Results. The tracks of single individuals when in an arena with one half illuminated and the other dark are shown in Figure 17A. The tick usually turned away from the lighted half of the arena and restricted its activity to the dark half.

When the tick was offered a range of light varying in intensity from bright to dim to dark, the subject invariably strongly avoided the lighted part and wandered in the dimly lighted and dark parts of the arena (Figure 17B).

When the arena was lighted by a divergent cone with high middle intensity ranging to dark at the periphery, two engorged and two hungry ticks were dropped in the middle of the arena with their anterior ends facing the source of light. Figure 18 shows the tracks of these ticks. Hungry ticks immediately turned back from the light, walked round the arena, and rested in the darkest, peripheral area. When disturbed, they moved only round the dark area; on coming to the lighted area they quickly turned back. Engorged ticks behaved in the same way but required from two to four minutes to perceive the light and finally to avoid it.

No adaptation to light was experienced, as ticks exposed to light prior to experimentation exhibited the usual avoiding reactions to laterally or horizontally directed light beams.

The reaction of hungry ticks to a light source from above, an overhead bulb of 100 watts, was then tested. Tracks are shown in Figure 19. When the light was switched on, the subject hesitated at first, then became agitated, quested with its fore legs, increased its rate of movement, and exhibited many turning reactions. At the same time it tried to avoid the light by pushing the anterior end of its body between the floor and the wall of the arena.

Discussion. Although *O. erraticus* is an eyeless tick, it appeared from these experiments to be sensitive to light. This sensitivity was of the nature of avoiding reactions, even to low light intensities. *O. erraticus*, therefore, is a negative phototactic species.

Reactions of ticks to combination of factors

In nature it is seldom that a single factor in the tick's environment exerts its effect independent of other factors. Certain factors, however, influence the tick's activity and behavior more than others. These experiments were designed to elucidate the relative importance of the various factors described above.

Temperature and humidity

Method. Hungry ticks were offered the usual arrangement with the exception that one half

of the arena had a favourable temperature and an unfavourable humidity while the other half had an unfavourable temperature and a favourable humidity. The combinations thus offered to the tick were 70° F. and 18% R.H. in one side and 115° F. and 95% R.H. in the other side, respectively.

RESULTS. The tracks of the tick in this arena (Figure 20) indicate activity on the side with the favourable temperature and the unfavourable humidity (70° F. and 12% R.H.). Although the tick on the first side did not move in straight lines but mostly took an undirected circular course, it strongly avoided the side with unfavourable temperature and favourable humidity (115° F. and 95% R.H.) and immediately turned back as it approached the separating line between the two halves.

It appears, therefore, that temperature may play a more important role than humidity in influencing the tick's behavior.

TEMPERATURE AND SMELL

METHOD. The hungry tick was then offered an arena in which one half was odorless but with a suitable temperature (80° F.) while the other half was scented with fresh rabbit's hair but with an unfavourable temperature (112° F.).

RESULTS. Normally, if other factors were within its range of tolerance, the tick preferred the scented side of the arena (p. 326). In the present arena the tick sharply avoided the scented side and was active on the side with favorable temperature and without any odor (Figure 21).

This indicates that a favorable temperature might be of more importance than host scent.

TEMPERATURE, HUMIDITY, AND LIGHT

METHOD. Now the tick was offered the choice of an arena that had one side with 70° F. and 95% R.H. (suitable temperature and humidity) but strongly lighted, and the other half with 115° F. 18% R.H. but in darkness.

RESULTS. The tick at first avoided the lighted side of the arena despite the favorable temperature and humidity. Later it became indifferent to both sides. Next it began strongly to avoid the side with unfavorable temperature and humidity and became active on the other side, disregarding the strong light (Figure 22).

These experiments appear to indicate that light is of less importance than temperature and humidity. Temperature may be the most important of all factors defining the tick's behavior and humidity appears to rank second in these factors provided that it is within the tick's range of preference.

SENSE ORGANS

Haller's Organ (Figure 23). Haller's organ, on the dorsal surface of the apex of the foretarsus, is a deep oval depression with thick, well chitinized walls. The opening of the depression is guarded by a group of four erect, stout bristles that become successively longer. These correspond to the anterior bristle group in *Ixodes ricinus* (Lees 1948). Another group of four bristles, longer than the distal group, with broad bases and sharply pointed, is present proximally. Both groups are typical tactile hairs. The floor of the depression is thickly chitinized and furnished with short, stout, sharply pointed, spinelike bristles arranged in rows that become successively longer towards the periphery of the organ. The posterior edge of the depression, which is also thickly chitinized, is produced over the cavity into four thin-walled, stiff spines that probably further protect its opening.

Haller's organ has been described from a number of ticks, particularly those in the genera *Ixodes* and *Haemaphysalis*. It was first regarded as an auditory organ provided with otoliths (Haller, 1881) but was later found by many workers to have a chemoreceptive function.

Other sensory organs on the legs of *O. erraticus* consist of small bristles distributed over the surfaces. These are relatively few in number and present no special morphological features other than those of ordinary tactile bristles.

Palpi and Mouth Flaps. At the apex of the palpi a cluster of short bristles are arranged on a differentiated area (Figure 24C). These sensillae are chemoreceptor and are composed of very short hairs with rounded tips and with thin walls.

Other than the palpal organs, the palps themselves, especially the dorsal surface, are richly furnished with tactile, sharply pointed bristles that are relatively long and become shorter toward the base of the basal segment. On the basis capituli, bristles are arranged in groups with tips directed anteriorly; an especially long pair of posthypostomal bristles arises ventrally just posterior of the base of hypostome. These are also tactile bristles.

In *O. erraticus* the mouthparts are protected by a dorsal mouth hood fused with lateral mouth flaps. The ventral as well as the dorsal surface of the hood and flaps are beset with numerous rows of bristles that are relatively long compared with others already described. These bristles are of the typical tactile form. Figure 24B is a transverse section of the hood illustrating the thick walled, stiff, tapering form of these bristles. Each is carried on an elevation of the cuticle and mounted in a deep, socketlike base ending in a canal penetrating the cuticle. At the base of this canal is found a special sensory cell (Figure 24B).

Other sensory organs are short tactile sensillae with rounded, somewhat deep bases that are distributed all over the body surface. These are alike in form and structure and are relatively sparse.

LOCATION OF SENSES IN *O. erraticus*

When testing the temperature and humidity reactions of *O. erraticus* it was observed that the tick waved its palpi and forelegs in rapid movements, apparently testing the immediate surroundings. This action indicated that the palpi and foreleg may contain special senses for perceiving temperature and humidity. The following experiments were undertaken to investigate this subject.

METHOD. The tarsal apex, which contains Haller's organ, of 10 specimens was covered with a thin, quick drying cellulose paint, vaselined, or amputated. In each case, the ticks were allowed some time to recover.

Treated ticks were then offered an arena with a favorable humidity but with one half with unfavorably high temperature and the other half within the normal temperature preference.

RESULTS. All three types of treated ticks strongly and persistently avoided the unfavorable half of the arena (Figure 25).

METHOD. The Haller's organ in another set of ticks was kept intact but the palpi, hood, and flaps were carefully covered with vaseline or with cellulose paint.

RESULTS. The subject avoided high temperature (Figure 26). The same reaction was displayed by ticks with non-functional Haller's organ and palpi.

This indicates that neither of these organs contain temperature receptors.

METHOD. The same experiment was then undertaken in an arena with uniform temperature and variable relative humidity, favorable on one side and unfavorable on the other.

RESULTS. The tick in this case also avoided the unfavorable humidity area (Figure 27A and B) indicating the Haller's organ and the palpal organs contain no special humidity receptors.

Lees (1948) however, suggested that the numerous short bristles on the forelegs of *Ixodes ricinus* are concerned with perceiving minute temperature differences in the surrounding air rather than temperature difference of the substratum. These bristles are rare on the legs of *O. erraticus*.

METHOD. Ticks with Haller's organs removed were offered an arena with one side scented with the scent of *Gerbillus p. pyramidum* and the other free of any odor.

RESULTS. The hungry tick walked freely from one side of the arena to the other (Figure 28). This shows that Haller's organ may be concerned with the perception of odors, *i.e.* chemoreceptors.

METHOD. Two sets of ticks, one with Haller's organ out of action and the palpi and mouth hood functional, the other with Haller's organ functional and palpi and hoods non-functional, were confined with a host.

RESULTS. The first group of ticks was able to suck blood and engorge when placed directly on the host. However, they were not attracted to the host when they are at a little distance. The second group of ticks, however, was unable to engorge and all died after about 24 hours. Apparently, therefore, tactile hairs on the palpi, mouth flaps, and Haller's organ, as well as the palpal organs, are concerned with host discrimination. Haller's organ may assist in host discrimination at a very short distance in a contaminated area, though the other organs perceive only what they actually contact. With removal of Haller's organ, *Argas persicus* is unable to discriminate hosts and imbibes any fluid, according to Hindle and Merriman (1912).

Although special organs sensitive to light could not be located, it appears that some must be present on the anterior half of the body inasmuch as hungry ticks facing a light turn away immediately, while engorged ticks, whose convex body may partially shade these receptors, turn more slowly from the light. Both hungry and engorged ticks were indifferent to a light shining from behind.

SUMMARY

The reactions of female *Ornithodoros erraticus* (Lucas, 1849) to five different environmental factors, temperature, humidity, smell, gravity, and light were investigated in the laboratory in order to provide background data for further field studies on the biology, ecology, and epidemiological significance of this species in Egypt.

Temperature.—In uniform temperatures of 70°, 84°, 94°, 104°, and 110° F. the subjects actively travelled in circles at 84° and 94° F. but were very sluggish at 104° and 110° F., moving with half the body lifted on the wall of the arena. Engorged females offered a combination of a high and a low temperature alternatives, avoid the high temperature. The intensity of avoiding reactions increases in proportion to the amount of temperature difference in the two halves of the testing arena. Hungry ticks move freely from one side of the arena to the other.

Humidity.—Reactions to humidity are influenced by the tick's feeding condition. Engorged females in a humidity range of 18%, 33%, 75%, 95%, 98%, and 100% R.H. are active in low and medium humidities (18% to 75% R.H.) but avoid high humidities (95% to 100% R.H.). With alternative humidities, 98%–18%, 95%–18%, 95%–33%, 95%–62%, 95%–75%, 95%–83% and 95%–100% R.H., the same behavior is displayed. In the last two combinations, the tick avoids both humidities. The optimum humidity condition for engorged ticks is 75% R.H. Hungry ticks prefer 95% to 100% R.H., their optimum appearing to be 95% R.H.

Preconditioning experiments indicated that the reactions of hungry individuals are influenced largely by their body's water balance. Hungry wet ticks first avoid the humid side of an arena,

but return to it when their body retains its normal water balance; desiccated hungry ticks rest in the humid side. Desiccated engorged ticks avoid the dry side while wet engorged ticks avoid the wet side.

Smell. Host finding is random. Hungry individuals detect a host only after coming into actual contact with it and engorge from any body region, particularly where there is little hair. Of hair of gerbils, guinea pig, rabbit, and dog, that of gerbils is much preferred. Host feces offers no special attraction.

Gravity. Hungry ticks are negatively geotactic and readily climb up a vertical tube. Engorged ticks are positively geotactic.

Light. Both hungry and engorged ticks are negatively phototactic and avoid light of any intensity. Hungry ticks do so immediately while the engorged ticks react more slowly. The convexity of engorged ticks possibly hides light receptor organs on the anterior of the body.

Sense Organs. The morphology of the sense organs is illustrated and described. Air temperature is perceived through the general body surface, possibly through the dorsal surface while that of the substratum is perceived through the ventral body surface. Humidity perception occurs through the body surface and is effected by the disturbance of the water balance after feeding. No special organs sensitive to light were detected but it appears that the anterior half of the body contains such organs. Haller's organ is chemoreceptive and concerned with host perception at a distance. Contact chemoreceptors, palpal organs, and tactile hairs of the palpi and mouth flaps, are concerned with host discrimination.

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BIOLOGY OF MEGACHILE RELATIVA CRESSON (HYMENOPTERA, MEGACHILIDAE) IN TRAP-NESTS IN WISCONSIN

J. T. MEDLER[1] AND T. W. KOERBER[2]

ABSTRACT

In 1952-56, 304 nests were obtained in artificial cavities made in sumac sticks. Cells per nest were 7.7 ± 3.1 (range, 2 to 14); usually each was made with 10 oblong-oval leaf pieces and capped with 3 circular ones. Summer generation nests were completed by July, and nests made later contained an overwintering generation. In cells transferred individually to glass vials, larval stages took 19 to 22 days at 15° C., 8 to 12 days at 22°, and 6 to 8 days at 27°. Pupal stages took 16 to 18 days at 22° and 6 to 9 days at 27° (no larvae pupated at 15°). Usually cells toward the inner end of the cavity contained female bees, those toward the outer end males, but in some nests all the bees were of one sex or the other. Very rarely were female cells constructed after male cells. Nesting sites at the edges of woodlands were preferred, at heights of 5 to 7 feet rather than nearer the ground, and a slight preference for ¼-inch rather than ⅜-inch holes was shown. Parasitic bees harbored in the nests were of three species, *Coelioxys banksi* Crawf., *C. lucrosa* Cress., and *C. moesta* Cress., but the wasp *Leucospis affinis* Say was the most serious parasite. Another wasp, *Melittobia chalybii* Ashm., attacked the trap-nests and was troublesome in the incubators because, upon emerging in one tube, it entered others through their corks to parasitize the *Megachile* larvae there. *Dibrachys* sp., with habits similar to those of *Melittobia*, was reared from some of the nests. Artificial nesting cavities may provide the flexibility needed for propagation of *Megachile relativa*, but research is needed on the problems of increasing its populations and concentrating them at alfalfa seed producing locations, as well as on evaluation of the effectiveness of this bee in pollinating the alfalfa seed crop.

Research on the biology and ecology of native bees in Wisconsin was undertaken with the objective of utilizing this basic knowledge, if possible, to increase the numbers of bees and bring about effective pollination of alfalfa. The study was needed because numerous field observations in relation to research on alfalfa seed production showed that a lack of pollinating activity was largely responsible for poor seed yields. Various systems of crop management, minor element fertilization, and application of insecticides increase seed yields somewhat in Wisconsin when used in association with favorable weather conditions, but a consistent method of seed production has been impossible without control of pollination.

The family Megachilidae includes species which are potentially valuable pollinators of alfalfa seed crops. Students of the Megachilidae have reported on a wide variety of nesting habits of the various species, including observations on nests made in tunnels in the ground, holes in logs, snail shells, hollow stems, and miscellaneous other natural cavities. "Artificial" nesting cavities have been used, such as hollow stems (Fabre 1915; Friese 1923; Balfour-Brown 1925), holes in logs (... k and Bolton 1946) and glass tubes (Hicks 1937; Frost 1943).

METHODS

Two types of artificial nests were tried in Wisconsin. A "domicile" type contained holes of various sizes. Several ¾" x 8" x 6" boards were bolted together and the holes were drilled across the grain at the interfaces. About two dozen holes were drilled in each domicile, the holes being staggered from opposite sides. The individual borings were examined by removing the bolts and separating the boards, or pulling out the glass tubes slipped into the holes. The holes were generally ¼ inch (6.25 mm.) and ⅜ inch (7.8 mm.) in diameter drilled to a depth of about 6 inches (150 mm.), or enlarged to fit 8, 9, and 10 mm. glass tubes (outside diameter).

A "trap-nest" type was made by providing a bundle of 8-inch lengths of sumac stems. The soft pith of a stem was drilled out to a depth of about 6 inches. Usually three stems with ¼-inch holes and three stems with ⅜-inch holes were placed in a bundle. The individual stems which were occupied were removed from bundles and split open to study the contents. The two types of artificial nests are illustrated in figure 1. Views of the nests opened for inspection are shown in figure 2.

Experience with the two types has led to the exclusive use of the sumac stems in recent research. Although the domicile type was very effective in providing nests of bees, certain disadvantages attended both the opening and closing of the boards and the examination of the domiciles in the field. Glass tubes were acceptable to the bees and observations on the progress of nest construction could be made. However, the

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technique was impractical for subsequent rearing studies because of the problem of obtaining individual cells. Also, the glass tube nests had considerable insect mortality, possibly due to excessive development of mold.

Our most effective method to study bee nesting was to place sumac-bundle trap-nests at various field stations in early spring and inspect them at periodic intervals during the season. Stems containing nests in various stages of construction were removed from the bundles, identified by code numbers, and brought back to the laboratory for study. The cells were usually transferred individually to small glass vials for rearing, or for time-temperature studies. Rearings were conducted at 27° C., 22° C., 15° C., and at room temperatures. A standard record sheet was used for each nest. It provided for notes on the ecology of the nest, illustration of the nest construction, and data on subsequent rearing of the insects. Records were also kept on the growth and development of larvae when feasible, and widths of head capsules of representative larvae were measured daily to determine the number of instars in the larval stage. In some instances the abundant material necessitated capping an unopened stem with a glass vial, and holding it for emergences. Such stems were opened later for study, but exact association of adults with cells could not be made.

FIG. 1.—The two types of "artificial" nesting cavities used in research on the nesting biology of bees in Wisconsin.

RESULTS

A number of species of Megachilidae have been studied in Wisconsin by means of the trap-

nests, but this report is concerned exclusively with *Megachile relativa* Cresson. Other species will be reported on in subsequent articles.

During the period 1952–56, a total of 304 nests of *M. relativa* was obtained for study. Data are summarized in Table 1. Using pieces of green leaf, the mother bee constructed a linear series of thimble-shaped cells each 10 to 12 mm. long. Circular leaf pieces were used to plug the nest entrance. In many nests the orifice plug was preceded by a filler of loosely packed leaf pieces and an inner plug adjacent to the last-built cell. Occasionally, the orifice plug and or the inner plug were faced with a smooth thin layer of clay or well-chewed leaf. The thickness of plugs varied greatly. Nests lacking a distinct plug were considered unfinished, but it is probable that most of such nests were brought back to the laboratory before the foundress bee had finished her activity.

Each cell was closed with a capping consisting of layers of circular leaf pieces. The usual number of pieces was 3, but as many as 11 pieces were recorded. The sides and bottom of a cell were made with oblong-oval pieces of leaf. About 150 cells were studied in detail. Table 2 shows the variation found in the number of leaf pieces used for the construction of cells. The data for the number of leaf pieces exclusive of capping pieces in 101 cells from $\frac{1}{4}$-inch holes showed 9.94 ± 2.12 pieces, and 29 cells from $\frac{5}{16}$-inch holes showed 11.69 ± 2.52 pieces. It is believed that the variation in the number of leaf pieces per cell reflects the different thickness of leaves from at least three species of plants commonly used, and inherent differences in the building techniques of various bees. However, these variables were integrated to produce a cell with a fairly constant inside diameter of about 5 mm.

The data for 148 finished nests in $\frac{1}{4}$-inch holes showed that 7.76 ± 3.14 cells, range 2 to 13, were constructed for the summer generation, and 7.71 ± 3.02 cells, range 2 to 13, for the overwintering generation. In 61 nests in $\frac{5}{16}$-inch holes, the summer generation nests had 7.71 ± 3.48 cells, range 3 to 14; the overwintering generation 7.50 ± 2.97 cells, range 2 to 13. The composite data for 209 finished nests of *M. relativa* showed 7.68 ± 3.07 cells, range 2 to 14.

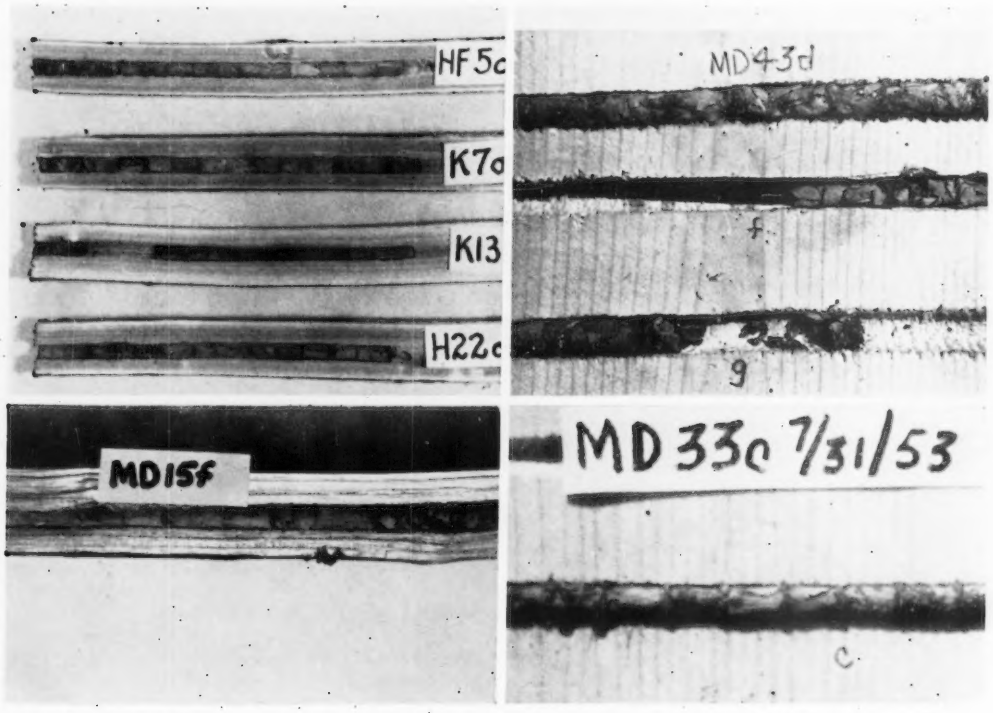

FIG. 2.—Artificial nesting cavities opened to show details of nest construction by *Megachile relativa* Cresson.

Although a maximum of 14 cells was found in a trap-nest, it is believed that a higher number would occasionally be recorded if a longer hole were provided. It should be mentioned that a trap-nest bundle sometimes contained several sticks with nests. It was not possible to ascertain whether or not a single bee was responsible for

the multiple nests, but such a possibility exists. Unfinished nests found side by side with finished nests strengthens the hypothesis that one foundress might construct more than 14 cells.

Exact information on the rate of cell construction, provisioning, and closing was not obtained but it is estimated that no more than two cells were built per day. Possibly, one cell per day was nearer the average rate of construction. The bees were inactive during rainy weather and were very active during hot sunny weather so the rate of construction varied from day to day. The summer generation nests usually were completed by early July. Those nests constructed in the latter part of July and during August contained the overwintering generation.

Each provisioned cell was about half-filled with a mass of pollen and nectar. When first placed in the cells, the provisions were semi-fluid, and sticky or viscous enough so that they did not flow out when the cells were inverted. The color ranged from creamy white through various shades of yellow to orange or sometimes brown. In some instances the provisions became sour or moldy. This condition was associated to some extent with prolonged periods of cold, wet weather.

TABLE 1

SUMMARY OF DATA OBTAINED FROM A STUDY OF 304 NESTS OF *Megachile relativa*, 1952–1956

Cells unsuitable for rearing study because of soured provisions, mold, injury, prior emergence, etc.	558
Cells transferred to individual vials, but rearing not accomplished*	406
Cells transferred to individual vials and rearing of adults successfully accomplished	
Megachile relativa	651
Leucospis affinis	240
Melittobia chalybii	127
Coelioxys spp.	21
Dibrachys sp.	5
Total cells	2008

*Many failures were caused by unsuitable conditions used in time-temperature research on larvae in diapause.

The source of provisions was from a wide variety of plants. *M. relativa* has been collected on the following flowers in Wisconsin: alfalfa, *Medicago sativa* L.; alsike clover, *Trifolium hybridum* L.; aster, *Aster* spp.; birdsfoot-trefoil, *Lotus corniculatus* L.; blackberry, *Rubus* spp.; black-eyed Susan, *Rudbeckia serotina* Nutt.; bull thistle, *Cirsium vulgare* (Savi) Tenore; buttercup, *Ranunculus* spp.; Canadian thistle, *Cirsium arvense* (L.) Scop.; daisy, *Chrysanthemum leucanthemum* L.; dandelion, *Taraxacum officinale* Weber; fireweed, *Epilobium augustifolium* L.; goldenrod, *Solidago* spp.; hawkweed, *Hieracium aurantiacum* L.; pearley everlasting, *Anaphalis margaritacea* (L.) Clarke; raspberry, *Rubus* spp.; red clover, *Trifolium pratense* L.; rose, *Rosa* spp.; spurge, *Euphorbia* sp.; sumac, *Rhus typhina* L.; sweet clover, *Melilotus officinalis* (L.) Lam.; sunflower, *Helianthus* spp.; white clover, *Trifolium repens* L. Although not common on alfalfa, *M. relativa* has been recorded tripping alfalfa flowers in northern Wisconsin, and was reported to do likewise by Peck and Bolton (1946) in Saskatchewan.

When a cell had been completely provisioned the foundress desposted a creamy-white egg on the surface of the mass of provisions. The egg was about $2\frac{1}{2}$ mm. long and 1 mm. wide, rounded at both ends and slightly curved. The egg hatched in 2 or 3 days, producing a weakly segmented almost transparent larva. The newly emerged larva was about 2 mm. long and slightly more than 1 mm. wide. It was somewhat dorsoventrally flattened with a projecting ridge along either side. The spiracular openings were on the dorsal surface of this ridge. On the basis of head capsule measurements it is believed that there are four larval instars. However only a very small number of larvae were reared from the egg stage and it is possible that there might be a very short first stadium, a few hours long, that was not detected. During the first two stadia the larva fed in an extended position, partly submerged in the semi-liquid mass of provisions. As the small larva fed it gradually became the color of its food. The provisions became dryer and were of a pasty consistency by the time the larva was in the third instar. During the later part of the second stadium and through the third stadium, the larva gradually became curved, so that the older third instar larva was crescent shaped. At that time the larva was about 5 mm. long and the ridges along the sides had disappeared. As the larva changed shape, its head was directed toward the inner end of the cell with the dorsal side of its posterior end at the outer end of the cell. At the beginning of the last stadium the larva was about one-half the size of a mature larva. At this stage it began to pass fecal pellets and grow very rapidly. By the time the larva was mature, it almost filled its cell, and the fecal pellets were crowded against the sides and into the corners of the cell. The mature larva began almost immediately to spin a cocoon of tough reddish brown silk, which very nearly filled the cell. The spinning of the cocoon usually required 2 or 3 days. When the cocoon was finished, the larva oriented itself with its head toward the mouth of the cell. This orientation is necessary for proper emergence of the adult bee as the adult would be unable to turn around in the narrow cell.

The larval stage probably takes from 12 to 14 days under field conditions. When reared at constant temperatures in the laboratory the larval stage took 19 to 22 days at 15° C., 8 to 12 days at 22° C. and 6 to 8 days at 27° C. Under field conditions the summer generation larvae

pupate 7 to 10 days after reaching maturity. The period between larval maturity and pupation in the laboratory required 7 or 8 days at 22° C. and 4 or 5 days at 27° C. Second generation larvae passed the winter in diapause in cocoons and did not pupate until the following spring. In the laboratory the pupal stage lasted 16 to 18 days at 22° C. and 6 to 9 days at 27° C. None of the larvae pupated at 15° C.

The adult bees did not leave their cells immediately upon emerging from the pupae but remained quietly in their cocoons for three or four more days. The wings and integument hardened during this period. Under field conditions all of the bees from one nest emerged at the same time. This situation was not duplicated in the laboratory. Table 3 shows representative nests from which individuals were reared and the sequence of male and female cells recorded.

The cells toward the inner end of the hole were occupied by female bees whereas those toward the outer end were occupied by males. It would seem that the bee building the nest is able to control the sex of her progeny so that the eggs deposited in the first cells produce females and the eggs deposited in the last cells produce males. Some nests contained either all females or all males, but in only two nests (21 and 22) were female cells constructed after a male cell.

Table 2.—Number of oblong leaf pieces used in the construction of individual cells in ¼-inch nests of *M. relativa*.

Nest Number	Cell Number											
	1	2	3	4	5	6	7	8	9	10	11	12
3	10	9	9	9								
23	14	15	11	10								
5	10	7	11	8	12							
6	13	10	12	12	12	11						
21		7	9	8		10	11					
12	12		10	13	17		18					
25				9		7	10	10				
38					10	9	10	9	10			
39		13		10	10	13		10	10			
15	10	13	8	12	10	9	13	10	13			
16	12	11	10		11	8	10		12	8	11	
17	10	10	9	9	10	12	11		9	9	9	
40			13	12	12	10	12	12	9	13	14	13
26			4	7	4	6	7	7	8		5	4

Table 3. Cell sequence of females and males of *M. relativa* reared from finished nests.

Nest Number	Cell Number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	♀	♀											
2	♀	♀	♀										
3	♀	♀	♀	♂									
4	♀	♀	♀	♂	♂								
5	♀	♀	♀	♂	♂								
6	♀	♀	♀	♂	♂	♂							
7	♀	♀	♀	†	♂	♂							
8	♀	♀	♀	♂	♂	♂							
9	♀	♀	♀	♂	♂	♂							
10	♀	♀	♀	♀	♀	♀	♀						
11	♀	P	♂	♂	†	♂	♂						
12	♀	†	♀	♀	†	†	♂	♀					
13	♀	♀	♀	♀	♀	♀	♀	♀	♀				
14	♀	♀	♀	♀	♀	♀	♀	♀	♂				
15	♀	♀	♀	♀	♀	♀	♀	♂	♂				
16	♀	♀	♀	†	♀	♀	♀	†	♀	♀	♀		
17	♀	♀	♀	P	♂	♂	♀	♀	♂	♂	♂		
18	♂	†	♂	♂	♂	♂	♂	♂	†	†	♂		
19	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	†	
20	♀	♀	♀	♀	♂	♂	†	♂	♂	♂	♂	†	
21	♀	♂	♂	♂	♂	♀	♀	♂	♂	♂	♂	♂	
22	♀	♀	♀	♀	♀	♂	†	♀	♀	♀	♀	†	†

P = parasitized cell; † = larva died during rearing.

The habitat data of the locations where trap-nests were accepted by *M. relativa* showed that this species had considerable preference for nesting sites at the edges of woodlands. Peck and Bolton (1946) found *relativa* frequenting the poplar habitat in northern Saskatchewan. According to Brown and Curtis (1952) the conifer-hardwood stands in Wisconsin are a part of one great community complex, arranged along an environmental gradient from xeric pioneer conditions to mesic climax conditions. *M. relativa* was common in trap-nests in northern Wisconsin and rare at southern locations. Though there is an abundance of extensive woodland habitats in northern Wisconsin and fewer in southern Wisconsin, more information on the ecology of the species is needed before this distribution pattern can be associated primarily with the woodland habitats.

A slight preference for $\frac{1}{4}$ inch holes as compared with $\frac{5}{16}$-inch holes was exhibited, and also 5-foot to 7-foot nesting situations were preferred to those placed near the ground.

There was some competition for the nesting sites, principally between the bees and wasps. In 29 nests, eumenid or pompilid wasps superseded *M. relativa* 18 times, usually after only two or three cells had been constructed by the bee. *M. relativa* superseded wasp nests nine times.

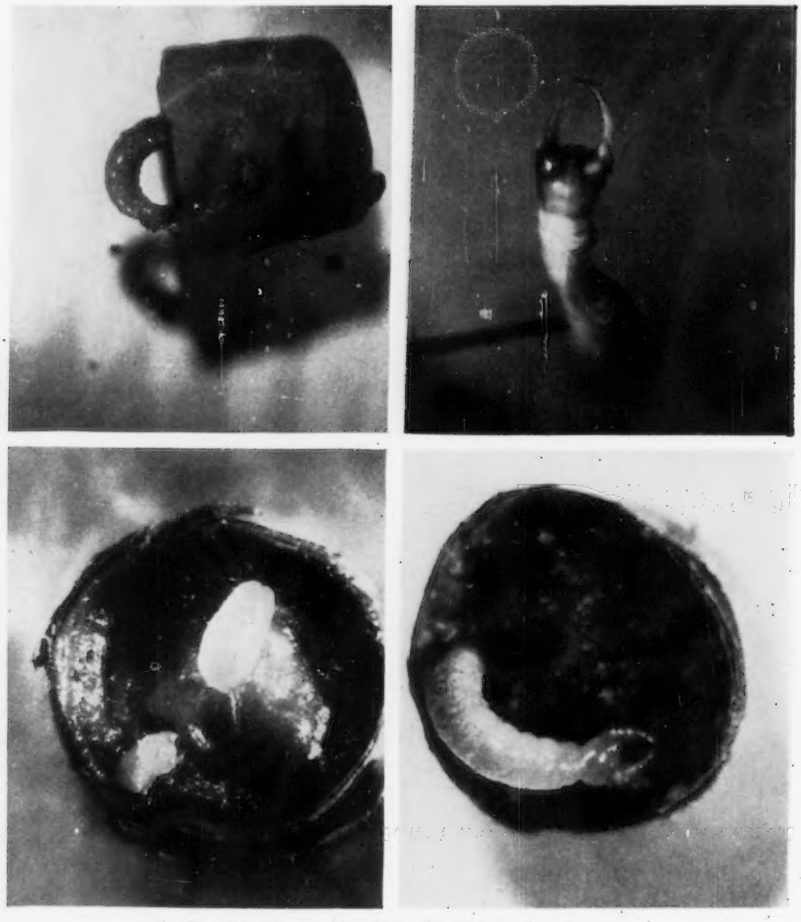

FIG. 3.—Views of *Coelioxys* larva in early stages.

In one $\frac{5}{16}$ inch stick *M. inermis* Prov. built above an unfinished 5-cell nest of *M. relativa*. One other $\frac{1}{4}$-inch stick set out on June 28, when opened on August 1, contained a 5-cell finished nest of *M. relativa* with pupae; but on top there was a 6-cell unfinished nest of the same species containing very small larvae. It was impossible to determine if the small amount of supersedure recorded was a result of actual

competition, or merely the appropriation of an abandoned nest.

The nests of *M. relativa* harbored three species of parasitic bees: *Coelioxys banksi* Craw., *C. lucrosa* Cress., and *C. moesta* Cress.[3] The female *Coelioxys* deposited an egg at the inner end of the *Megachile* cell while the cell was being provisioned. The first instar *Coelioxys* larva was elongate and cylindrical with a rather large head and large sharp-pointed mandibles. It burrowed its way to the surface of the mass of provisions usually by following the side wall of the cell. The second instar *Coelioxys* larva had a pair of horn-like dorsal spines and long sharp-pointed mandibles. At this stage the posterior part of the larva remained in its burrow in the pollen mass. The anterior part of the body was arched so that the head faced the surface of the mass of provisions. The long, curved, sharp-pointed mandibles were used to churn up the pollen mass, killing the *Megachile* larva in the process. At the second moult the *Coelioxys* larva lost its big head capsule and long mandibles and appeared very similar to a *Megachile* larva. Figure 3 shows the early stages of *Coelioxys*. The parasite larva consumed the provisions, spun a cocoon similar to a *Megachile* cocoon, and pupated to emerge as an adult at the same time as the *M. relativa* bees in other cells of the nest. Table 4 gives the rearing data obtained from parasitized nests. The rearing record of two *Coelioxys* species from nest 39 is of interest.

The most serious parasite in the trap-nests proved to be the large chalcoid wasp, *Leucospis affinis* Say. The *Leucospis* female was able to lay eggs through wood by means of its long ovipositor. An egg deposited in a *Megachile* cell by this method hatched into a smooth, white, distinctly segmented larva with a very small head. This larva fed externally on a mature *Megachile* larva or pupae, leaving nothing but an empty skin and head capsule. The *Leucospis* larva passed small, round, black fecal pellets during its entire larval period, and pupated inside the *Megachile* cocoon without spinning a cocoon of its own. Only one *Leucospis* adult emerged per *Megachile* cocoon. All of the cells, or the majority of cells in a parasitized nest, contained *Leucospis*. In the partially parasitized nests, the emergence of bees and wasps took place at the same time.

The trap-nests were attacked also by *Melittobia chalybii* Ashm.. Apparently this small wasp enters a cell when it is being built or provisioned, and remains there until the *Megachile* larva matures, at which time eggs are laid externally on the host. In 24 examples where the host was entirely consumed, 139.1 ±65.2 parasites, range 61 to 282, were produced per host larva. *Melittobia* placed in vials with bee larvae exhibited behavior similar to that described by Buckell (1928). It was impossible to determine the extent of *Melittobia* parasitism in the field because wasps emerging in our incubators entered through the corks of other rearing tubes and parasitized the larvae from other nests.

Another wasp, *Dibrachys* sp., with habits very similar to those of *Melittobia*, was reared from some of the nests. This is a larger wasp producing about 25 adults per *Megachile* larva.

Table 4. Cell sequence of *Coelioxys* parasites in nests of *M. relativa*.

Nest	Cell Number											
	1	2	3	4	5	6	7	8	9	10	11	12
31	♀Cl	♂M	P	P								
32	♀M	♀M	♀M	♂Csp								
33	♀Cm	♂M	♀M	♂M								
34	♀M	♀M	♀M	♀M	♀Cm							
35	♀M	♀M	♀Cb	♀M	♂M	♀M						
36	♀M	P	♂M	♂M	♀Cb	♀Cb	♀M					
37	♂M	♂M	♂M	♂M	♂M	♂Csp	♂Csp	P	•			
38	♂M	♂M	♀Cb	♂Csp	♀M	♀M	♀M	♀M	♀M			
39	♀Cb	♀M	♂M	♂M	♂M	♂M	♀Cb	♂M	♂M	♂Csp	♂Cl	
40	♀Cb	•	♀M	♀M	♀M	♀M	♀M	♀M	♀M	♀M	♀M	♀M

♀ = female; ♂ = male; P = *Melittobia chalybii*; • = unprovisioned cell; † = larva died before maturity; M = *M. relativa*; Cb = *C. banksi* Cwfd.; Cl = *C. lucrosa* Cress; Cm = *C. moesta* Cress.; Csp = not determined.

The only positive record on the nesting habit of *M. relativa* appears to be the observation of Hicks (1926) on a single unfinished cell associated with a foundress. Also, the record of Guignard (1887) of *brevis* nesting in sunflower stems probably applied to *relativa*, according to Peck and Bolton (1946). Mitchell (1935) found *relativa* at a window of a shed containing logs of firewood, and suggested a nesting association with the wood.

[3] Determined by T. B. Mitchell.

By means of the trap-nest technique 300 nests of *M. relativa* were studied in the period 1952–56. Records showed conclusively that in northern Wisconsin, this species prefers to nest in a ¼ inch or $\frac{5}{16}$-inch hole at the edge of the woodlands. Nests averaged 8 cells, each cell constructed with 10 oblong leaf pieces, and capped with 3 circular leaf pieces.

Considerable information on the biology and ecology of the species was obtained during the period of this study; but the objective of using this basic knowledge to bring about more effective pollination of alfalfa has not yet been realized. Future pollination research is being planned, since it would seem that the trap-nest technique could be applied to this problem in northern Wisconsin. Sumac-bundles might be placed at various locations to obtain an abundance of nests, which might then be concentrated at alfalfa fields so that the emerging bees would be available for pollination.

A method of using log trap-nests was considered as practical by Peck and Bolton (1946) but in need of modifications to conform more closely with the biological needs and habits of the bees. The sumac bundles may provide greater flexibility than logs, and they seem to be well suited for the propagation of *M. relativa*.

It is believed that parasitism by *Leucospis affinis* would be the most serious problem associated with any attempt to concentrate the population of *M. relativa*. A method of preventing oviposition by this parasite possibly would be needed as a control measure. Although unimportant in the field during our present study, parasitism by *Coelioxys* spp. and *Melittobia chalybii* might become a problem as host populations were increased and concentrated.

It is evident that the use of *M. relativa* to bring about more effective pollination of alfalfa must wait until more research can be conducted on the problem of increasing populations, concentrating the populations at seed producing locations, and evaluating the effectiveness of the species in the pollination of the seed crop. The trap-nest method should be a useful technique to enable further study on this basic problem on insect abundance and behavior.

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LIRIOMYZA GUYTONA[1]: A NEW SPECIES OF AGROMYZID LEAF MINER

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ABSTRACT

This dipterous species has been collected in Alabama, Florida, and Texas. Its leaf-mining larvae cause serious damage to foliage of tomato, bean, squash, cucumber, and other garden and greenhouse plants.

The leaf-mining larvae of the fly described herein have been found damaging garden and field crops in Lee County, Alabama. The severity of the damage in tomatoes, beans, crucifers, and cucurbits increased considerably during the 1956 growing season. Specimens of this species have also been taken from cucurbits in Florida and tomatoes in the Rio Grande Valley, Texas.

Male. Bright yellow and black. Head yellow, ocellar triangle and occiput black. Black of occiput reaching compound eye and uniting with black of ocellar triangle. Both vertical setae on dark, inner on lighter brown than outer. Antenna

[1]Named for Professor F. E. Guyton, API, Auburn, Alabama. Accepted for publication January 17, 1958.

[2]I am deeply grateful to Dr. Kenneth E. Frick, State College of Washington, for the loan of specimens and for reviewing the manuscript.

yellow, arista black. Thorax with mesonotum shiny black, finely punctate, black not extending laterally to callus or presutural setae, curving strongly mesally at the transverse suture; supra-alar on black at margin of yellow, the black curving strongly mesally at the outer postalar and passing just posterior to the inner postalar, but not quite reaching the scutellum. Outer postalar on black at the margin of the yellow. Scutellum with small black triangles, basal scutellar bristle on black, at the margin of the black and yellow. Humerus with small black spot, humeral setae on yellow. Anepisternum yellow, wide sub-rectangular dark area on antero-ventral margin, posterior margin with narrow dark line. Katepisternum with black triangle, no posterior marking; hypopleuron black. Pteropleurite with narrow black stripe anteriorly, basal portion with yellow border. Femora and coxae yellow tinged with brown basally, tibia and tarsi brown. Wings hyaline. Abdominal tergites black, bordered with yellow posteriorly and laterally.

Head. (In lateral view as in Figure 1.) Gena midway between vibrissal angle and posterior margin, about one-sixth eye height. Eye large, about two-thirds wide as high. Genovertical plates very slightly raised above eye margin; two lower and two upper fronto-orbital setae, the lower fronto-orbitals and the lower upper fronto-orbital about equally spaced. About three orbital setulae on each genovertical place. Antennae with third segment rounded, broad as long, setulae minute; arista about as long as eye width, swollen on basal one-sixth.

Thorax. All setae long; four dorsocentral bristles, fourth one-third longer than third, third twice as long as second, second only slightly longer than first. First, second, and third approximately equally spaced, fourth one-third more removed from third than third is from second. Five to seven setae in intraalar row posterior to the transverse suture. Intraalar present, subequal to first dorsocentral; inner postalar about one-half as long as outer postalar. Acrostichal setae about sixteen in number, in four irregular rows extending posteriorly midway between third and fourth dorsocentrals; humerus with three setae plus humeral.

Wing. About twice as long as wide. Costa terminating at M_{1+2}, second segment about twice as long as first, second segment at least three times as long as third, third and fourth segments approximately equal; m-m cross vein about its own length from r-m, perpendicular to the pentultimate section of M_{1+2}; ultimate section of M_{1+2} about five times as long as the pentultimate section; ultimate section of M_{3+4} about three times as long as the pentultimate.

Size. Wing length, 1.3 mm.

Female. Larger, wing length 1.5 mm., head with gena one-fifth eye height; thorax with nineteen acrostichals, six setae in intraalar row, intraalar present, slightly larger than acrostichals; wing with second costal segment three and one-half times the length of the third, m-m cross vein at a moderate angle to the pentultimate section of M_{1+2}; abdominal tergites with broad posterior band of yellow, seventh segment conical, truncate, shining black.

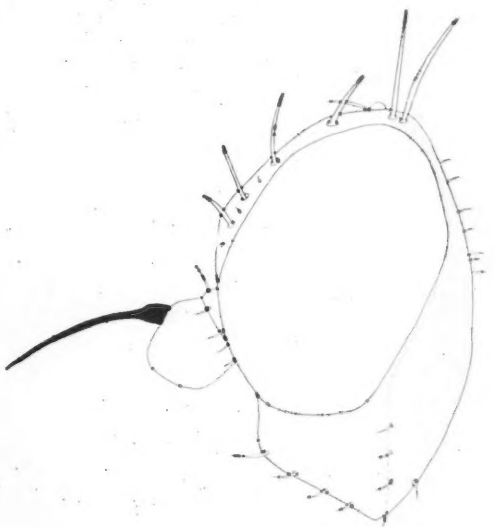

FIG. 1.—Lateral view of head of paratype of *Liriomyza guytona* n. sp.

Holotype: Auburn, Alabama, April 20, 1957, deposited in the U. S. National Museum. *Allotype:* Topotypical, April 25, 1957, also deposited in the U. S. National Museum. *Paratypes:* All topotypical reared from beans April, 1957, by the author. Paratypes have been deposited in the collections of the U. S. National Museum, the University of Florida, the University of California, the Alabama Polytechnic Institute, the British Museum, Dr. Kenneth E. Frick, State College of Washington, and the Author.

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SEXUALES AND EGGS OF THE SPOTTED ALFALFA APHID[1]

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ABSTRACT

The spotted alfalfa aphid, *Therioaphis maculata* (Buckton), produces some sexuales in the fall and winter. They are produced more freely in the warmer part of its range than in the colder areas. Eggs are laid sparingly and none hatch. Lack of viable eggs prevents gene recombination and also leads to the extinction of this species in the northern part of its range each winter.

The spotted alfalfa aphid, *Therioaphis maculata* (Buckton), has now occupied an area in North America about 1,800 miles north and south by 2,400 miles east and west. It has persisted throughout the year as far north as Kansas and central Utah, but in locations colder than these it seems to have been killed out each winter. The failure of the spotted alfalfa aphid to survive winter in the northern part of its range indicates that this species does not produce normal eggs.

The production of eggs by an aphid provides the species with a hibernating stage in which it can survive winter, and also provides for gene recombination. Normal parthenogenetic reproduction in aphids proceeds without reduction divisions so does not result in gene recombinations. All the forms except the egg and the male are produced in this way. The male is produced by parthenogenesis from a cell that has gone through a peculiar reduction division in which only the X chromosomes are reduced. There is a good general discussion of this by White (1945). Eggs and sperm are produced by meiosis, and the egg must be fertilized to develop. Aphids in which the phenomenon has been studied have produced sexuales in response to short day-length combined with low temperature. Marcovitch (1924) found that the strawberry root aphid, *Aphis forbesi* Weed, produced sexuales when exposed to only 7½ hours of light per day. Davidson (1929) reported that *Aphis rumicis* L. produced sexuales under short-day conditions—some even at greenhouse temperature. Wadley (1931) worked with the greenbug *Toxoptera graminum* (Rondani), and was able to make it produce both males and oviparous females when illumination was less than 12 hours per day and the temperature averaged 70° F. or less.

METHODS

Populations of spotted alfalfa aphid were sampled from time to time through the fall and winter of 1956–57 at several locations in southern California. Samples were taken by beating or sweeping any part of the field where a suitable population could be found. The aphids were shaken through a screen, preserved in a lactic acid-alcohol-water mixture, and examined under a dissecting microscope.

Total adults, males, normal apterous oviparae, and alate oviparae were counted. Only adults were counted since sexuales generally cannot be distinguished while immature. About 2,000 adults were usually examined from each place on each sampling date, although smaller counts were made if it was not possible to collect that many aphids. The largest count was 8,027.

Most (86.4%) of the sexuales taken were apterous oviparae. These varied somewhat in appearance, particularly in the extension of the abdomen, but generally looked about as would be expected for this species (fig. 1), except that the anal plate in the oviparae is entire rather than bilobed as in the other forms of this species. Alate oviparae, an abnormal form, made up 9.8% of the sexuales found. They also varied in shape. Males made up 3.8% of the sexuales recorded. Those found were alate, smaller than most alate viviparae, and had conspicuously dark antennae with the usual large number of sensoria. The anal plate is bilobed.

Males are more difficult to distinguish from the viviparae than are the oviparous females, so it is probable that a larger proportion of males than of oviparae were overlooked. In addition, aphid males usually do not live as long as females, so the proportion of males given above (3.8% of the total sexuales) is probably lower than their actual occurrence. Oviparous females of this species become orange in color as their eggs mature so are relatively easy to distinguish.

FIELD OCCURRENCE OF SEXUALES

Five locations on the Colorado desert were sampled, two in the Coachella Valley (Riverside Co.) and three in the Imperial Valley (Imperial Co.). Data from the five locations were averaged. The average per cent total sexuales on various sampling dates are shown in figure 2. Mean and minimum temperatures and day-length expressed as hours possible sunlight are shown in the same figure. Temperature records are from Weather

[1]Paper No. 1019, University of California Citrus Experiment Station, Riverside, California. Accepted for publication January 29, 1958.

Bureau Climatological Data (1956, 1957). Hours possible sunlight (Marvin, 1905) give only general indication of day-length since the figure shown does not take into account either topography or twilight.

Data shown in figure 2 indicate that the spotted alfalfa aphid produces sexuales in response to short day-length and low temperature, but that it produces relatively few of them. The highest percentage recorded in any field in this area was 6.7% sexuales in a sample taken January 4, 1957, from a location south of Westmoreland, Imperial Co. Even this does not approach the percentage of sexuales found normally in a species that is actually entering the egg stage to survive the winter.

It would seem that sexuales first appeared on the desert near the end of October and peaked about a month to six weeks later. Sexuales almost disappeared from the population by the end of January, possibly because of the warm weather during the first half of that month. A cold spell at the end of January was followed by the reappearance of sexuales in mid-February. These had disappeared by early March.

The coefficient of correlation between the percentage of sexuales and the mean temperature 15 days previous to the sampling dates was −0.11, and the probability of correlation due to chance alone was found to be greater than five times out of ten. The coefficient of correlation from the same sample data and the mean temperatures 7 days previous to sampling was −0.52, which gave a probability of correlation, due to chance, of one time out of ten.

Similar data from one location at Lakeview, California, near Riverside, are shown in figure 3. These data appear to be more erratic than do those in figure 2. This is because data in figure 3 are from a single field. Data in figure 2 are the means of figures from five locations. Lakeview, Riverside Co., is intermediate in location and climate between the coast and the desert. The appearance of sexuales there generally followed the same pattern as it did at the desert locations. At Lakeview, as in the two desert valleys, the spotted alfalfa aphid was able to maintain rather large populations all winter by parthenogenesis.

Figure 4 shows similar data from a strictly coastal location, Del Mar in San Diego Co. The climate there is moderate with small daily variation in temperature. Fungus infection generally kept the aphid population sparse in these fields so that it was impossible to collect samples on some of the proposed sampling dates. Sexuales appeared in this location at about the same times as at the interior locations, but the percentage remained low.

Figure 5 shows data through the fall at two colder locations. Hinkley is in San Bernardino Co. near Barstow on the Mojave Desert, considerably higher and colder than the Colorado Desert locations shown in figure 2. Bishop is in the Owens Valley, Inyo Co., just east of the Sierra Nevada mountains, and is colder than Hinkley. Cold weather at both locations froze the alfalfa down to ground level so that it was not possible to sample the spotted alfalfa aphid populations through the winter. The aphids produced few sexuales at Hinkley and even fewer at Bishop.

Production of sexuales in this species seems to occur in response to a combination of short day-length and low temperature, as expected from work with other aphid species. Sexuales have not been found to make up as large a part of the fall population as they do in species that normally pass the winter in the egg stage. At its highest point the average percentage of sexuales for all locations reached 2.3.

Early in the season, males made up a larger proportion of the sexuales found than they did later on. On November 6, males constituted 13.7% of all sexuales. Males declined through the winter until on January 4 they made up only 0.7% of all sexuales. No males were found after that date.

FIG. 1.—Oviparous female of spotted alfalfa aphid laying an egg.

Spotted alfalfa aphids produce sexuales in highest percentages and greatest numbers in relatively warm, dry areas in which they are able to maintain relatively high populations through the winter by parthenogenesis. In cold areas in which it would be most advantageous to the species to have overwintering eggs, the sexuales seem to be produced sparsely. The very mild coastal climate also induces few sexuales.

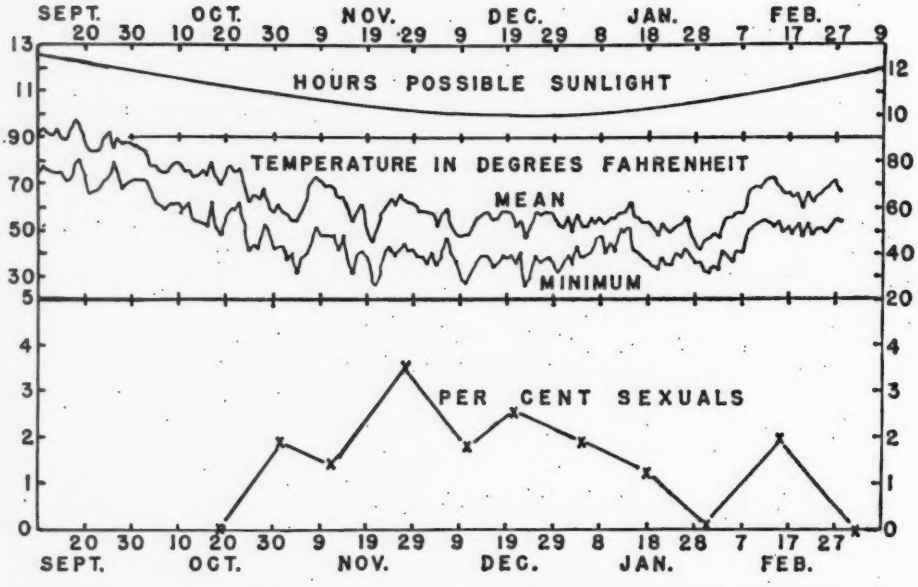


FIG. 2.—Mean percentage of sexuales in samples of spotted alfalfa aphid collected in five fields in the Coachella and Imperial Valleys, Colorado Desert, California, during the winter of 1956–57.

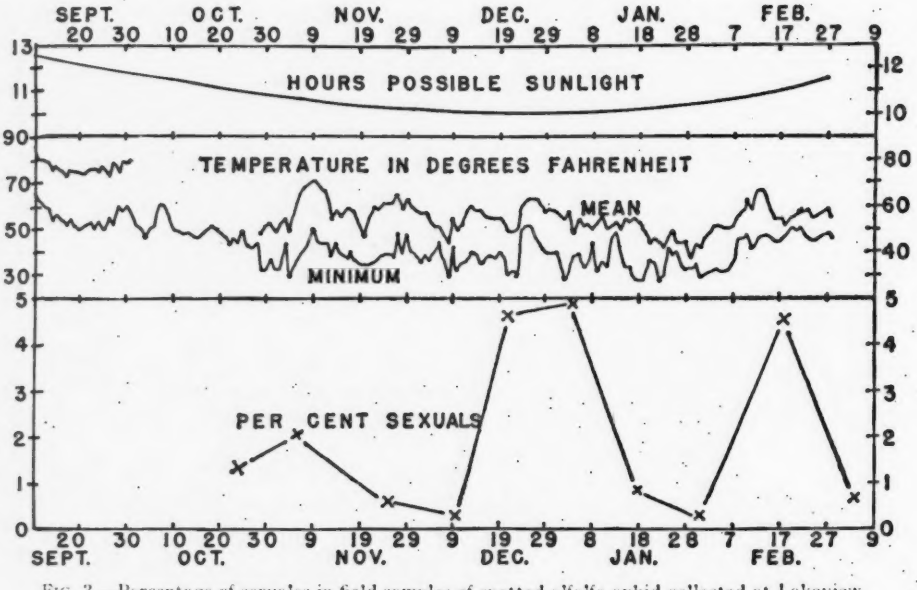
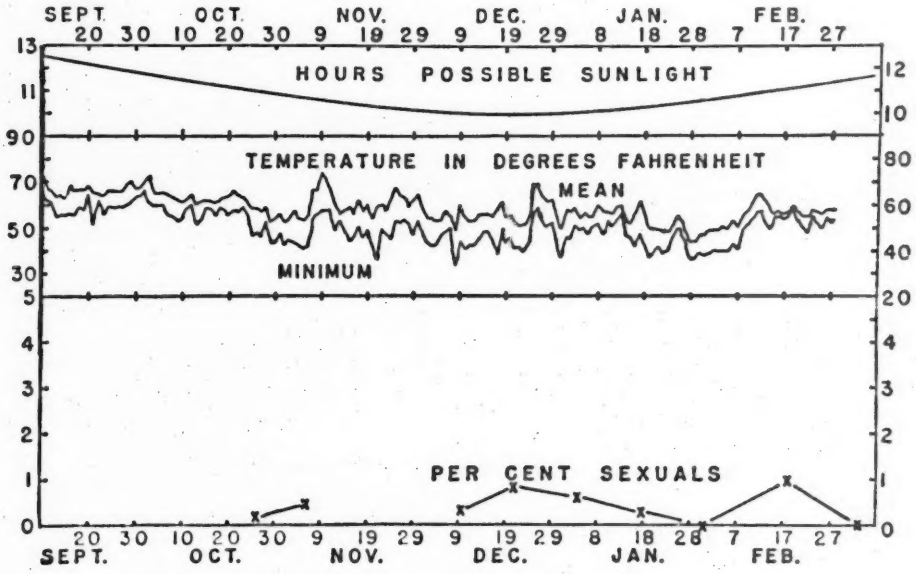


FIG. 3.—Percentage of sexuales in field samples of spotted alfalfa aphid collected at Lakeview, near Riverside, California, during the winter of 1956–57.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HOURS POSSIBLE SUNLIGHT
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MEAN
MINIMUM
PER CENT SEXUALS

FIG. 4.—Percentage of sexuales in field samples of spotted alfalfa aphid collected at Del Mar, coastal southern California, during the winter of 1956-57.

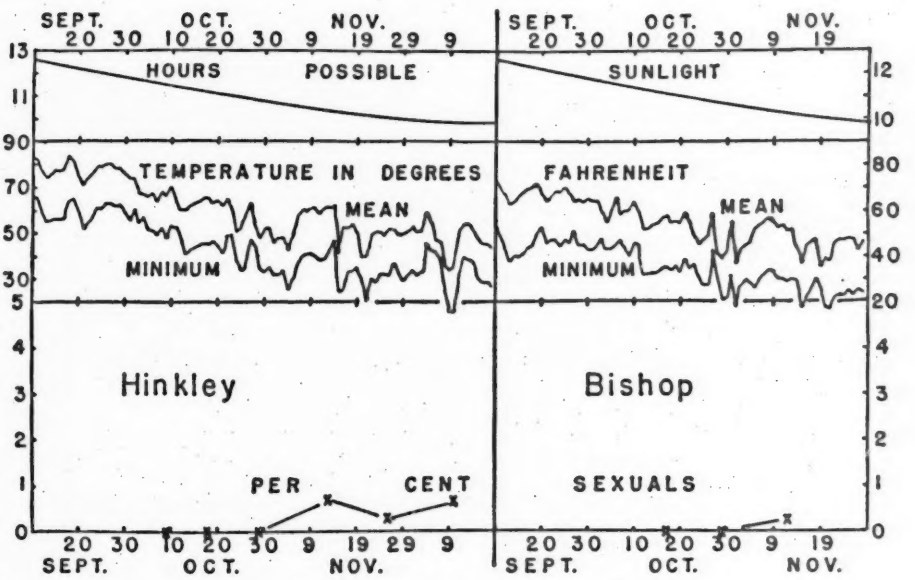

FIG. 5.—Percentage of sexuales in field samples of spotted alfalfa aphid collected at Hinkley on the Mojave Desert and at Bishop in the Owens Valley, California, during 1956-57.

OVIPOSITION AND EGGS

On eight dates from October 25, 1956, to February 21, 1957, apterous oviparous females were gathered in the field and caged on potted alfalfa plants. Part of these were placed in the greenhouse and the rest maintained outside, at Riverside. In all, 763 oviparae were caged as long as they lived on alfalfa plants. Some of them laid eggs. Figure 1 shows one of these females laying an egg. Egg deposition was atypical in that the eggs were deposited at random on leaves or stems rather than carefully in protected places, as is normal for aphids.

The 763 females laid only 137 eggs or 0.18 eggs per ovipara. Since the oviparae were field-collected, some of them certainly had laid eggs before they were confined. Even so, the oviposition record is very poor. A few of the normal-appearing apterous oviparous females could be seen to contain both eggs and developing embryos. None of these young were ever born, and older oviparae were sometimes observed to contain dead, blackened young. Most apterous oviparae appeared to contain eggs only. Alate oviparae, which are an abnormal form not used in oviposition tests, seemed, ordinarily, to contain both eggs and embryos. A few oviparae were confined singly. One of these laid three eggs.

None of the 137 eggs hatched. Normally, aphid eggs are pale when laid but soon turn black as the embryos develop. The change to black indicates that the egg is fertile. None of the spotted alfalfa aphid eggs turned black. They all turned brown and then became shrunken and dried and dead.

DISCUSSION

It would appear that the spotted alfalfa aphid is in the process of losing its sexual forms. The sexuales are produced erratically, in rather small numbers, and in the wrong locations. Males are in short supply and may not function at all. Many oviparous females are abnormal, having wings or short abdomens or containing embryos in addition to eggs, and the few eggs they do produce do not hatch.

Since the spotted alfalfa aphid does not seem to produce viable eggs it is, in effect, entirely parthenogenetic. This means that it can pass the winter only where the climate is mild enough that active forms can find live plant tissue to feed on through the winter. This aphid will not be able to overwinter in the northern part of its range but will have to move north each summer as the greenbug does.

The absence of viable eggs means that there will be no gene recombination in this species. Resistance to an insecticide has already appeared in this species (see Stern & Reynolds, 1958) in the form of a strain showing about 4x resistance to parathion. This character was established in the species in southern California a little more than two years (1954–1956) after the spotted alfalfa aphid was first found there. This period covers 60 to 70 generations from introduction, and probably not more than ten successive parathion treatments on any appreciable part of the population. It is probable that only a single specimen of spotted alfalfa aphid was introduced into North America and that the entire present population is descended from her. This population seems to have been entirely susceptible to organic phosphate insecticides when these were first used against it. Thus it would appear that such resistance as we have is the result of mutation and subsequent selection to produce resistant clones. There is no evidence of the appearance in North America of clones differing in appearance from our original specimens.

In biparental species, factors for resistance which have appeared in various individuals throughout the population may combine to produce resistant individuals and then superresistants. This recombination cannot occur in the spotted alfalfa aphid. Resistance or any other change in the population can only come about through the selection of a superior clone.

The spotted alfalfa aphid should be slow to change, and the appearance of superresistant populations should be delayed unless this should come about through the mutation and selection of a single new gene for superresistance.

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THE MEASUREMENT OF ADULT POPULATIONS OF THE EYE GNAT, HIPPELATES PUSIO[1]

RICHARD P. DOW AND GLENN A. HUTSON

ABSTRACT

A bait trap of new design is described. It was used in southwest Georgia to capture large numbers of the *Hippelates pusio* group (*H. pusio* Loew and *H. bishoppi* Sabrosky); other species also captured were easily recognized and removed from collections. In large catches where *H. bishoppi* was also taken, it was found practical to obtain satisfactory estimates of *H. pusio* by weighing the collections at a fixed humidity and determining the ratio of the species in samples of about 100 specimens. When *H. bishoppi* drops below 10% in the catches, the numbers of *H. pusio* can be estimated with the same reliability by identifying smaller samples. *H. pusio* reached its seasonal peaks from July through September; *H. bishoppi* showed a similar pattern but appeared to decline more rapidly. *H. pusio* was caught in small numbers when traps were located at a distance from any known attractants, with the object of sampling hypothetically uniform areas, but when traps were set beside animal enclosures it was taken in large numbers. The numbers of gnats trapped beside chicken pens were significantly correlated with the numbers of fowl in the pens. Net and aspirator collections made near and on mammals consisted almost entirely of *H. pusio*. The proximity of animal enclosures had little or no effect on the trap catches of *H. bishoppi*, and since this species was never taken under circumstances that would prove attraction to a mammalian or an avian host, its numbers should not be included with those of *H. pusio* for epidemiological purposes. The numbers of gnats observed about human subjects were found unsuitable for calculating a prevalence index, even though they were found to be correlated with the size of trap catches in nine communities with a wide range of gnat prevalence during a period when trapping showed a marked seasonal change. Gnats observed on and about the heads of children were significantly more abundant when the subject had a history of conjunctivitis, also when the child was "active in the open" rather than "inactive in the shade."

The eye gnat, *Hippelates pusio* Loew, is a common pest in many parts of the southern United States. It is attracted to the skin and hair of various mammals including man, and frequently occurs about the eyes of man, especially when there are crusts of secreted matter. Because of its close association with the eye, it appears to be at least an occasional vector of human conjunctivitis due to *Haemophilus aegyptius*, the Koch-Weeks bacillus. With the ultimate object of determining whether this bacterial disease could be controlled by reducing the numbers of eye gnats, various studies on the biology and control of *Hippelates* were conducted at the Thomasville Field Station of the U. S. Public Health Service, Thomasville, Georgia, from 1949 to 1953. This article, the third on these investigations, discusses various studies made to test and refine methods of measuring eye gnat prevalence.

H. W. Kumm (1935) measured the prevalence of the Neotropical *Hippelates flavipes* Loew by making collections on ulcers of donkeys, but the usual method of measuring the prevalence of *H. pusio* and its California congener *Hippelates collusor* (Townsend) is by traps baited with fish, egg, or liver. This technique was originally developed by D. C. Parman (1932) and R. W. Burgess (1935). Further contributions have been made by E. R. Tinkham (1951).

[1]From the Communicable Disease Center, Bureau of State Services, Public Health Service, U. S. Department of Health, Education, and Welfare, Logan, Utah. Accepted for publication March 3, 1958.

HOST RELATIONSHIPS OF *Hippelates*

When prevalence trap collections made in southwest Georgia in 1950 were carefully identified they were found to include occasional specimens of *Hippelates bishoppi* Sabrosky, a species closely related to *H. pusio* and not quickly separated from it with assurance. In the following year *H. bishoppi* exceeded 50 percent of some catches. It therefore became essential to know whether *H. bishoppi* was also attracted to human eyes and whether, in estimating the vectoring potential of *Hippelates*, this species could be counted with *H. pusio*. Some observations of J. T. Bigham (Dow, Bigham, and Sabrosky, 1951, page 265) had suggested that *H. bishoppi* might not be zoophilous and this possibility was supported by collections made on mammalian hosts in southwest Georgia.

More than 30 collections of *Hippelates* were made from man and other mammals in 1951, partly by aspirator and partly by net. Most of the specimens were *H. pusio*, but there were seven *H. bishoppi*, all females. These were all taken in catches made by sweeping a net as close as possible to a cow or hog. Six *H. dissidens* (Tucker), three *H. pallipes* (Loew), one *H. particeps* Becker, and one *H. plebejus* Loew were also caught in the same way. Since *H. dissidens*, *H. particeps*, and *H. bishoppi* are not otherwise known to be associated with mammals, and since the net might easily have caught an insect that was in nearby vegetation or merely flying close to an animal, no real importance could be attached to these records. It therefore seemed wise to

make all further collections with an aspirator which would permit specimens to be taken from precise areas of the host's body. Another limitation of the 1951 collections was the fact that 13 of them had been made after September first. *H. bishoppi* is relatively less common than *H. pusio* in the fall of the year, and therefore, to increase the chances of finding it on an animal host, it was desirable to make collections in the spring or summer.

Twenty-three collections were made with an aspirator on various mammals in the spring of 1952, 6 entirely from the eyes and 12 entirely from other parts of the body, including sores. No *H. bishoppi* occurred in any of these collections (table 1). At each collecting locality, net collections were made routinely, mostly by sweeping weeds and grass. In this way, *H. bishoppi* was shown to be present in the vicinity when 13 of the 23 aspirator collections were made.

There is additional support for the hypothesis that *H. bishoppi* is not an eye fly in the differential response of *H. bishoppi* and *H. pusio* to bait putrefied under aerobic *vs.* anaerobic conditions, also to exposed *vs.* freshly poured bait (unpublished studies). Further evidence that *H. bishoppi* differs from *H. pusio* in the sources of its nitrogenous food is provided by some casual trapping done in May 1952 near Savannah, Georgia. Here, in eastern Chatham County, where annoyance of man by eye gnats is considered very slight, liver-baited traps set in four different locations took more than 350 specimens of *H. bishoppi* and only one of *H. pusio*.

Table 1.—Aspirator collections of *Hippelates* on mammals, Thomas and Brooks Counties, Georgia, April and May, 1952

Host	No. of collections[a]	Times *H. bishoppi* in vicinity	*H. pusio*	Other *H.* species
Man	5	3	30	0
Dog	4	3	59	0
Cow	9	4	121	1 *H. saundersi* Kumm
Mule	3	2	89	1 *H. pallipes* (Loew)
Goat	2	1	37	0

[a]A collection is counted here as all the specimens taken from a single mammal on one day.

DEVELOPMENT OF TRAPS

Wooden Traps.—Unpainted wooden traps with sides of composition board (figures 1 and 2), based on "the simple box trap" of Burgess (1935), were used for all the routine prevalence trapping in 1950. Four modifications of the Burgess box trap were developed in the Lower Rio Grande Valley of Texas in the course of studies made in 1947 by Mr. George B. Vogt and Mr. Judson U. McGuire. One improvement was to place a funnel of cellulose acetate in the mouth of the collecting jar to hinder the escape of the trapped gnats. The second change, made practical by the introduction of the funnel, was to mount the jar upside down on the top of the trap. The third was to place the bait dish on a shelf directly under the collecting jar. The fourth was to put cotton in the bait dish to prevent the drowning of gnats in the bait. At the Thomasville Field Station, one further change was made. The shelf for the bait dish was extended to the front of the trap and the large hole in the front half was covered with ordinary house screening (readily penetrable to gnats) in order to keep large flies out of the collections.

There were various objections to the modified Burgess box trap. Though the changes apparently increased the ability of the trap to retain gnats, they also limited the amount of bait odor which could escape to the outside. A second criticism was the difficulty of maintaining unpainted wooden traps for use in an area as moist as southwest Georgia. A third objection was the probability that, with the box in a fixed position, the wind direction would strongly affect the amount of bait odor released. Finally, it was later realized that the distribution of the catch values was extremely skewed (see, for example, table 5, second column).

Metal Traps.—A metal trap which surmounted the above objections was first developed in the summer of 1950 and slightly modified thereafter (figures 1 and 3). It was made from an old-fashioned tin-plated dinner pail, 5 inches high and 7½ inches in diameter. The entire bottom was cut out of the pail, and replaced by a horizontal partition of ordinary house screening soldered into place about 1½ inches from the bottom. This served as a support for the petri dish, 20 mm. deep, which was used for bait. Three legs, of ⅜-inch rod, were soldered on the outside. A conical collar of sheet metal, 2¾ to 3¼ inches in diameter, was soldered to the margin of a hole, 2½ inches in diameter, cut in the cover of the dinner pail. This collar helped to hold in place the inverted one-pint glass fruit jar, used as the collecting chamber, which actually rested on the rim of the hole in the cover. All of these metal parts, except the screening, were painted with aluminum paint. A funnel was made of cellulose acetate with a hole at the apex

about $^{3}/_{8}$ inch in diameter. It was originally fitted to the mouth of the collecting jar, later cemented to a jar lid from which the center had been removed, and, finally, rigidly bound between two rings of metal, also cut from jar lids. This metal-rimmed cone was held on the jar by means of the threaded ring manufactured to hold the lid, and needed only to be plugged with cotton to hold the catch of gnats for removal to the laboratory.

Comparison of Wood and Metal Traps.—In a simple field test, two wood and two metal traps, each placed about 10 feet from any other, were operated in an area of short grass for a period of nearly 4 hours. The numbers of *Hippelates* of the *pusio* group were 23 and 60 in the wood traps, and 208 and 422 in the metal. The wood and metal traps were further tested on a slowly revolving turntable, 4 feet in diameter. In one test there was an average of 46 *H. pusio* in each wood trap and an average of 118 in the metal. In the other there was an average of 88 *H. pusio* in each wood trap and an average of 112 in the metal. The smaller difference between the two kinds of traps when rotated is believed to be the result of operating them so close to one another that the effect of releasing different amounts of attractant was reduced, and emphasis was given to the catching and holding capacities of each design.

OPERATION OF TRAPS

After 1949, all traps were routinely operated for a period of 4 hours during the day. The restriction as to daytime operation was necessary because tests showed that some gnats would escape from traps left set overnight, perhaps mostly because there was no light to hold them in the collecting chamber. Traps were always set on the ground, and, to avoid extremes of heat and light, were placed routinely in the shade of trees. Radiation of heat from the soil did not appear to reduce their effectiveness in southwest Georgia, but observations made in southern California by E. R. Tinkham (1951) show the need of placing the trap well above the ground in hot, desert situations.

FIG. 1.—Wooden and metal traps for *Hippelates*. The wooden trap on the left is the modified Burgess box trap used in 1950.

The bait used regularly from 1950 to 1953 was always made of pork liver. The basic formula was: 1 lb. ground liver, 1 lb. water, 1 oz. crystalline urea. Put in glass fruit jars and allowed to putrefy at room temperature, the mixture appeared to reach a stable condition in about 2 weeks. By preparing many small batches, thoroughly mixing all the successful lots, and deepfreezing this master mix in suitable containers, it was possible to have a bait that was uniform for the duration of a long study. Whether or not a master mix was used, each trap was

baited with a standard scoopful of the undiluted bait (about 25 ml.). This was poured on a layer of cotton in a petri dish.

The collections made by liver-baited traps in southwest Georgia consisted predominantly of *H. pusio* and *H. bishoppi*. Both are members of the *pusio* group, which, with few or no exceptions, was not otherwise represented in the catches. Most of the trapped specimens of both species were females, males averaging less than 10 percent of the collections. Other species of *Hippelates*, such as *H. proboscideus* Williston and *H. particeps* (Becker), were never represented by more than a few individuals. The catch of an unscreened trap could contain a large mass of blowflies, and phorids and borborids could be comparatively abundant in the smaller catches of screened traps. In general, however, no matter how large the catch, the numbers of insects other than *H. pusio* and *H. bishoppi* tended to remain very small.

Seasonal Occurrence of H. pusio and H. bishoppi.—In 1950, an epidemiological study of conjunctivitis was conducted in nine communities in and near Thomas County, Georgia. The collection of case history records and other data was concentrated in 122 selected blocks, and accordingly the same blocks were chosen for sampling the prevalence of eye gnats. From information obtained in 1949, it was known that more *Hippelates* would be caught if the traps were set beside animal enclosures. Since it would obviously be impossible to find equivalent attractants in each block, it was decided to locate all traps not less than 50 feet from potential attractants such as animal and poultry pens and places used for cleaning fish and disposing of garbage and waste wash water. Wooden traps were used. They collected an average of only 25 specimens of the *pusio* group per trap setting, and the size of the collections was subject to extreme variation. Where enough traps had been set, however, they appeared to give satisfactory information on the local and seasonal prevalence of eye gnats.

Of all the nine communities studied in 1950, Barwick had the highest catches of *H. pusio*, the seasonal peak of this species occurring in July and August (table 2). The rainfall in August and September of that year was below normal for points both east and west of Barwick, and presumably for Barwick as well. This may have hastened the decrease of *H. pusio* that normally occurs in the fall. In 1953, for instance, the numbers of trapped gnats were comparatively low in August but high in July and September.

The seasonal occurrence of *H. bishoppi* in the Barwick trap collections of 1950 was similar to that of *H. pusio* except that *H. bishoppi* became proportionally less frequent after August. The relative scarcity of *H. bishoppi* in September is confirmed by the records of 1951, and these findings agree with the observations of J. T. Bigham in Florida which also show a more rapid decrease in *H. bishoppi*, though earlier in the season (Dow, Bigham, and Sabrosky, 1951).

Occurrence of Gnats in Relation to Animal Pens.—In 1950, two of the trap sites in Barwick were inadvertently located within a few feet of chicken pens. The catches of the *pusio* group (*H. pusio* plus *H. bishoppi*) made at these two sites from March to November were only 2 and 3 percent *H. bishoppi*. At the eight sites distant from a known attractant, *H. bishoppi* made up from 8 to 24 percent of the *pusio* group. At the sites near animal enclosures there was a higher average number of *H. pusio*, but not of *H. bishoppi* (table 3).

In 1951, 20 traps were operated routinely at fixed sites, 10 beside animal pens and 10 distant from known attractants. Complete identification of the catches of three selected days gave results similar to those of 1950. On June 21, the percent of *H. bishoppi* in the *pusio* group ranged from 10 to 42 at the sites near animal pens, and from 49 to 96 at the sites away from attractants. (On this occasion, the average number of *H. bishoppi* was much higher at the sites distant

Table 2. Seasonal occurrence of *Hippelates pusio* group in baited traps operated at 10 sites, Barwick, Georgia, 1950[a]

Month	No. of trap catches	Mean *H. pusio* per trap catch	Mean *H. bishoppi* per trap catch	Percent *H. bishoppi*
March	40	49	4	7 9
April	20	1	< 1	9 1
May	40	13	1	6 6
June	50	56	4	6 2
July	30	600	43	6 7
Aug.	50	346	35	9 3
Sept.	30	45	2	3 3
Oct.	50	22	< 1	0 9
Nov.	30	16	< 1	0 4
March-Nov.	340	128	10	7 5

[a] In the 10 largest catches, each with more than 800 gnats, the total number was estimated from the weight, and the numbers of *H. pusio* and *H. bishoppi* were estimated from a sample of 100 specimens.

from attractants instead of being similar at both types of site.) The comparatively high percentages of *H. bishoppi*, also evident in the catches made on July 20, are believed to be due to the composition of the bait. This was uniform throughout 1951 because it was all taken as needed from a frozen master mix of various lots. It differed from most of the bait used in 1950, however, because perhaps half the total volume of this master mix had not been shaken routinely during putrefaction. This circumstance, supported by experiments made in 1951 and 1952 (unpublished), provides a possible explanation of the relatively high percentages of *H. bishoppi* trapped in 1951.

In 1952, as part of a special test made on July 23, 112 traps were operated in groups of four at 28 different sites in the town of Barwick. Fourteen of the sites were beside animal enclosures and 14 were distant from known attractants. Again the traps beside animal enclosures took both a much higher mean number and a much higher percentage of *H. pusio*.

A special analysis of the data from 1951 and 1952 was made by calculating regressions of the numbers of *H. bishoppi* on the numbers of *H. pusio* taken in the same catches. To reduce skewness in the distributions and to make variances more homogeneous, all numbers of these species, plus one, were transformed to their com-

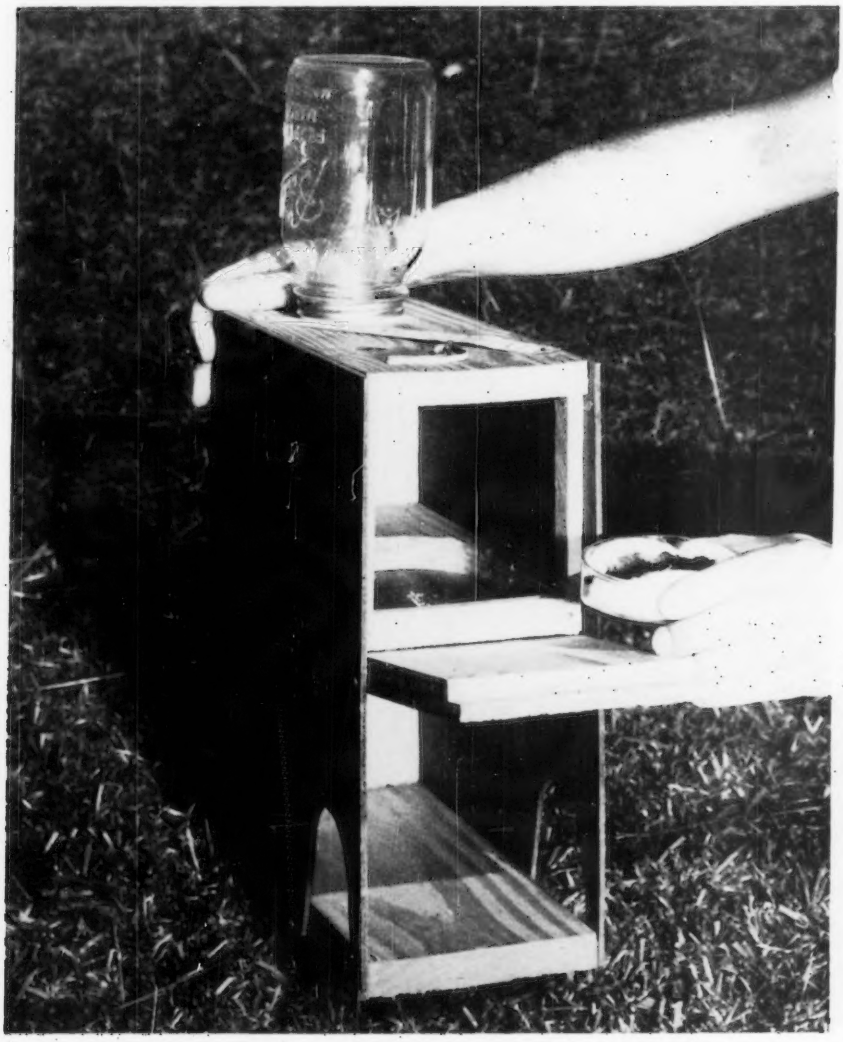

FIG. 2.—Wooden trap for *Hippelates*, with front opened to show how bait dish is introduced.

mon logarithms (Bartlett, 1947). It was found that in the traps near animal enclosures, the catches of *H. pusio* and *H. bishoppi* varied more or less independently, but in the traps distant from animal enclosures their numbers were more distinctly correlated. Thus, on a given day, *H. pusio* and *H. bishoppi* were more likely to be trapped in the same ratio if the trap was not located near an animal enclosure. From this analysis as well as from the actual trap data, it is concluded that animal enclosures are not specifically attractive to *H. bishoppi*.

partially correlated with the number of fowl they contained, there was no other known feature to account for the results of this test.

The principal conclusion to be drawn from the various studies of trapping is that traps for *H. pusio* should be placed near the natural attractants. This procedure discards the advantage of operating the traps under similar conditions but increases the likelihood of making large catches of *H. pusio* and assures a minimum percentage of *H. bishoppi*. On the other hand, since the catch of a trap placed beside a chicken pen

Table 3.—Occurrence of *Hippelates pusio* group in traps near and distant from known attractants, Barwick, Georgia, 1950–1952

Dates	No. of traps	Location of traps	Mean *H. pusio* per trap catch	Mean *H. bishoppi* per trap catch	Percent of *H. bishoppi*
March-Nov. 1950	2	near chicken pens	328	8	2 6
March-Nov. 1950	8	away from attractants	78	11	12 1
June 21, 1951	10	near animal pens[a]	372	139	27 1
June 21, 1951	10	away from attractants	109	297	73 2
July 20, 1951	10	near animal pens[a]	686	63	8 4
July 20, 1951	10	away from attractants	219	67	23 4
Sept. 25, 1951	10	near animal pens[a]	2,004	25	1 2
Sept. 25, 1951	9	away from attractants	630	29	4 4
July 23, 1952	56	at 14 sites near animal pens[b]	79	17	17 7
July 23, 1952	56	at 14 sites away from attractants	30	22	42 5

[a]8 chicken, 2 hog.
[b]8 chicken, 4 mule, 2 hog.

Occurrence of Gnats in Relation to Chickens.—In spite of a minimum of direct observation, there is strong evidence that domestic fowl are attractive to *H. pusio*. This relationship was the subject of a special test made in the towns of Boston, Barwick, and Pavo, Georgia, on September 2 and 3, 1953. Fifty-five traps were operated beside chicken pens which contained known numbers of chickens and other domestic fowl, and 30 traps were run at sites distant from known attractants. The collections of gnats were dried and weighed. They were not identified but were probably more than 90 percent *H. pusio*, even at the sites away from chicken pens, because the test was made in September. There was found to be a close relationship between the number of domestic fowl in the pens and the weight of the gnats caught in the traps beside these enclosures (table 4). This was further investigated by an analysis of variance which used logarithmic transformations of the original data. The common regression of weight of gnats on number of fowl was strong, and the regressions for each day were also strong and had similar slopes. All of the chicken pens were essentially similar, and although their size was is significantly correlated with the number of fowl kept in the enclosure, it is important, in locating traps to compare different areas by a prevalence index, to balance the representation of pens that have flocks of similar size.

Table 4. Relation of trap catches of gnats to proximity of fowl pen and to numbers of fowl therein, Boston, Barwick, and Pavo, Georgia, September 1953

No. of fowl	Mean weight of catches (mg.)
0[a]	38 1
1–10	41 4
11–20	91 5
21–30	90 4
31–50	111 6
>50	158 0

[a]Traps distant from any animal enclosure.

ANALYSIS OF TRAP CATCHES

As soon as large collections of *Hippelates* were encountered, it was clear that some way to

estimate their size would be needed. It appeared that volumetric measurement would be affected by potential compaction of the specimens, and that the success of counting aliquot fractions would depend on precise division of the catches. Consequently, studies were made of weighing whole collections. In these investigations it was found that the weight of dried *Hippelates* could vary nearly 10 percent with changes in the relative humidity. For example, one collection of dried gnats was weighed at intervals without regard to the duration or stability of the atmospheric conditions existing in the laboratory. Its weight was found to be very significantly correlated with the relative humidity at the time of weighing, ranging from 105 mg. at 35 percent relative humidity to 114 mg. at 72, 78, and 86 percent relative humidity. This change of weight, which appears to mark the gain and loss of atmospheric moisture, can take place very rapidly. A collection which had been kept in an incubator at a temperature of about 120° F. weighed 185 mg. when first removed to the air of the laboratory on a day in July. An hour later it weighed 196 mg. and 2 hours later, 201 mg. The maximum weight noted, 4 hours and 15 minutes after the first weighing, was 204 mg. This experience indicated that if collections were weighed immediately upon removal from a drying oven, weights of reasonable consistency could be obtained without air conditioning.

In a special investigation of the accuracy of estimating numbers of gnats from their weight, 36 collections taken in Barwick, Georgia, on June 21 and September 25, 1951, were weighed and counted in an air-conditioned room maintained at 54 to 62 percent relative humidity. After all insects not *Hippelates* of the *pusio* group were removed from the collections, the remaining specimens of *H. pusio* and *H. bishoppi* were identified in lots of 25 and weighed in lots of 500. In the separate weighed lots, the percentage of *H. bishoppi* ranged from 0 to 96. When the numbers of *H. bishoppi* in these lots were plotted against the corresponding weights, no correlation was apparent. It was therefore

FIG. 3.—Metal trap for *Hippelates*, disassembled to show cover, bait dish, and 1-pint collecting jar with threaded ring and metal-bound cone of cellulose acetate.

concluded that the average weights of *H. pusio* and *H. bishoppi* are not distinctly different, and that satisfactory estimates of the total gnats in mixed collections could be made without regard to the proportions of *H. pusio* and *H. bishoppi* which are actually present.

The formula which has been recommended for estimating the number of gnats in a given weighed collection is âW, in which W represents the observed weight of the collection, and â represents a constant which estimates the true (population) constant and is calculated from: $\hat{a}\Sigma W^2 = \Sigma WN$, N being the number of the gnats in each sample collection and W their weight, as above. To obtain â for use in routine investigations, a small number of collections should be weighed and counted under the standard conditions that will be used for weighing the rest of the trap catches. In the case of the 36 study collections weighed in milligrams at 54 to 62 percent relative humidity, the value of â derived from the total weights and numbers was 7.236. Multiplying each observed weight by this constant gave estimates of the total gnats in each of the 36 collections that ranged from 79 to 107 percent of the actual number, but were within 10 percent of the actual number (49 to 3,076) in 33 out of 36 cases.

Table 5. Frequency distributions of trap catches and attraction counts, 1950 study

No. of gnats	Times observed in trap catches	Times observed in attraction counts
0	596	508
1	155	32
2	87	62
3	47	25
4	45	6
5	27	76
6	34	7
7	18	0
8	17	4
9	14	0
10–19	83	33
20–29	40	6
30–49	38	1
50–99	34	0
100–500	24	0
501–1412	3	0

Provided that *H. pusio* and *H. bishoppi* are randomly distributed in the collections that contain both species, it is possible to estimate the numbers of *H. pusio* by identifying a small sample of each catch. The size of this sample, which will depend in part on the accuracy desired, can be determined from tables of confidence limits for the binomial distribution. When a sample size of 100 specimens was tested on the *estimated* numbers of gnats in the 35 study collections which contained more than 100 specimens, the estimated total of *H. pusio*, 24,761, was found to be only 1.8 percent less than the actual number.

A further point in regard to estimating the number of *H. pusio* is that for the same degree of accuracy, much larger samples must be identified as the percentage of either species approaches and exceeds 10. This situation strengthens the argument for trapping *H. pusio* near natural attractants because reducing the percentage representation of *H. bishoppi* makes it possible to estimate the numbers of *H. pusio* with equal accuracy from smaller samples.

ATTRACTION COUNTS

For special studies like those of Kumm (1935), it may be possible to measure the prevalence of *H. pusio* by making collections on a mammalian host other than man. This method is not considered practical, however, for a large-scale epidemiological study. Tractable animals belonging to private individuals are not likely to be available at suitable times and places, and hired or purchased animals are likely to introduce complications aside from logistics.

First Study of Human Attraction Counts.—In 1950, when great variability was being encountered in the catches of the wooden traps, it was suggested that a study be made of the numbers of eye gnats which could be counted on or about human beings. Accordingly, from September 8 to December 1, inclusive, the men who operated the bait traps also made observations on the numbers of gnats around persons.

In making this study, it was soon realized that satisfactory counts were not so difficult to obtain as had been expected, but it was necessary to supplement the counting by estimating, even in the range of 5 to 10 gnats. These attraction counts included not only those gnats which had alighted on the subject but also those which were flying in his immediate vicinity. The observers were directed to obtain five or more such counts whenever they trapped in a community. They were urged to concentrate their efforts on children, but they could not always find enough persons of any age outdoors along their route.

From an epidemiological viewpoint, attraction counts may be considered as sample values that estimate the contact between man and eye gnats. They may also be considered, like trap catches, as sample values of that fraction of the adult eye gnat population which is seeking nitrogenous food. Thus, to the extent that this activity remains a constant fraction of the life of an individual gnat, an index based on attraction counts should be a fixed fraction of the eye gnat population. Since no estimates of total population are available, neither attraction counts nor trap catches can be compared directly with the population parameter. All that is possible is to compare one type of observation with the other.

In all the trap collections analyzed in this study, the counts represent the *pusio* group and include

H. bishoppi. When the catches from Barwick were identified to species, however, the *pusio* group was found to be more than 98 percent *H. pusio* (table 2, Sept., Oct., Nov.). In the attraction counts, *H. pusio* was the only species of small fly likely to be observed (table 1).

The frequency distributions of both the trap catches and the attraction counts were found to be extremely skewed (table 5). To offset the effect of this irregularity in the statistical analyses, each number of gnats, plus one, was transformed to its common logarithm. Another feature of the data was the unequal distribution of the numbers of trap catches (4 to 47 in a single community per week) and, similarly, of the numbers of attraction counts (1 to 28 in a single community per week). To compare these unequal numbers of observations, the trap catches and the attraction counts were averaged for each week of the study in each community. The

Table 6. Relation of trap catches and attraction counts, 1950 study*

Community-week means of trap catches		Mean no. of gnats per trap catch	Mean no. of gnats per attraction count
Range of means	No. of means		
0·0–1·0	19	0·47	0·48
1·1–5·0	28	2·91	1·16
5·1–10·0	17	7·51	1·34
10·1–25·0	17	16·67	2·16
25·1–129·5	11	56·59	4·94

*After the means of the trap catches (averaged by week for each community) had been grouped according to their magnitude (columns 1 and 2), all the individual trap catches associated with each range of means were used to form a corresponding mean number of gnats per trap catch (column 3). The attraction counts associated with each range of means were averaged similarly (column 4). No logarithmic transformations were used in preparing this table.

basic data for these community-week means can be arranged to show a progressive increase in each measurement (table 6). Graphically the association does not appear very strong, but the correlation coefficient of the means themselves is 0.60 and exceeds the 1 percent level of significance.

Further analyses of the data have indicated that better sampling would have increased the value of the correlation coefficient, also that there was a significant relationship between single attraction counts and the catches of the nearest trap.

Second Study of Human Attraction Counts.—A second study of attraction counts was made in September 1953 with the cooperation of a nurse familiar with the conjunctivitis occurring in southwest Georgia. Her observations were made outdoors on children, most of whom were less than 7 years old. Besides counting (plus estimating) the number of gnats on or flying about the head of the child, and noting the race, sex, state of activity, and location of the subject with respect to shade, she examined the eyes, and when it was possible, asked for history of conjunctivitis. The observations were made in the three towns of Boston, Barwick, and Pavo on six different days, five times on the day of the bait trapping with which they were to be compared, and once on the day preceding. An average of 18.5 attraction counts was obtained in each town on each day, but no method used to analyze the data showed any correlation between trap catches and attraction counts.

This apparent lack of relationship between bait and human attraction might be the consequence of an insufficient number of observations, but other factors are considered more important. In 1950, the observations of people were made in or near the blocks where the traps were set; the analyses included not more than five attraction counts made near one trap on any given day; and finally, a point of great importance, there

Table 7. Mean attraction count (gnats per person), 1953 study

	Cases of conjunctivitis	Not cases of conjunctivitis
Children active in the open	5·0 (60/12)	2·7 (205/75)
Children inactive in the shade	3·4 (84/25)	2·2 (354/163)

were large differences in the abundance of gnats both by community and season.

The 333 attraction counts made in September 1953 provide acceptable information on eye gnats in relation to man because they were collected by one individual at times and places with relatively small differences in the prevalence of gnats. In noting which children had conjunctivitis, the nurse recorded whether her diagnosis was confirmed by history of illness and whether it depended, at least in part, on the presence of palpebral crusts. Since palpebral crusts have been shown to be useless in case finding (Dow and Hines, 1957), the 28 children who exhibited this sign and did not have a positive history of conjunctivitis are placed in a separate group and excluded from consideration as cases. The 42 cases remaining, 41 of which had a positive history, had a mean attraction count of 4.1 gnats. This figure is significantly higher than 2.3 gnats, the mean attraction count of the 263 negative children. (For the tests of significance, each attraction count, plus one, was transformed to its common logarithm.) The mean attraction count of the 28 children with crusts, 5.0 gnats, was also

significantly different from the mean for the negative children. The fact that children with cases and children with crusts were both highly attractive to gnats suggests that the common basis of greater attraction is the purulent matter secreted by the eye.

Of the 305 children considered as cases or as negative subjects, only 30 were noted as active in the shade or inactive in the open. Consequently, neither activity nor shade could be evaluated separately. It was possible, however, to compare "active in the open" with "inactive in the shade" in the 275 remaining subjects (table 7). In the cases of conjunctivitis, the mean attraction count was much higher for children that were active in the open. In the negative children, it was not so much greater for children that were active in the open, but the difference was shown to be significant.

In spite of the relatively small number of observations, it is clear that the mean attraction count was subject to considerable variation. Some of this was clearly associated with the condition of the eyes, and some with the location and state of activity of the person observed. In a large-scale epidemiological study, these factors might be partially controlled by making more frequent rounds of observations and by excluding the less frequent categories of people. Because some rigorous plan to minimize variation must be adopted and adhered to, it would seem unwise to employ attraction counts for a prevalence index in any prolonged study. On the other hand, the mean attraction count should be of real use in a quick evaluation or rapid survey.

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THE PASTURE AEDES OF CENTRAL AND NORTHERN CALIFORNIA. SEASONAL HISTORY[1]

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ABSTRACT

Aëdes squamiger and *A. dorsalis* breed on the intertidal marshes of the coast. The former, a univoltine species which undergoes obligate summer diapause, occupies the marshes primarily during the winter and early spring; its diapause appears irreversible and is terminated by low winter temperatures, perhaps also by shortened photoperiod. *A. dorsalis*, a multivoltine species, occupies the marshes primarily during the summer; winter dormancy of its eggs is believed to be a facultative diapause induced and terminated by environmental factors of which temperature is primarily important. *A. nigromaculis* and *A. melanimon* (=*A. dorsalis* in part of authors before 1955) are found in water resulting from intermittent irrigation in the inland valleys. Both were found to be multivoltine breeders which probably undergo an egg diapause similar to that of *A. dorsalis*. Except for insignificant overlapping, these two species occupy separate ecological niches in the same general environment and do not compete directly with one another.

The pasture *Aëdes* of central and northern California can be subdivided according to habitat. *A. dorsalis* (Meigen) and *A. squamiger* (Coquillett) take advantage of periodic tidal flooding on coastal saltgrass-pickleweed marshes. *A. melanimon* Dyar and *A. nigromaculis* (Ludlow) benefit by intermittent inundation of inland pastures and other irrigated crops.

COASTAL MARSH AND SALTGRASS PASTURE BREEDERS

The salt marsh breeders inhabit an essentially natural environment. Excluding abatement work, these mosquitoes are little affected by the activi-

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ties of man. Spatially, they occupy an identical habitat; nevertheless, they are effectively separated in nature by time. *A. dorsalis* is the primary summer marsh occupant while *A. squamiger* is dominant during the winter. However, there is a considerable overlap so that these species occur together during the spring of each year.

In order to gain better knowledge of how the coastal marshes are utilized by their mosquito inhabitants, a typical salt marsh near Bolinas, California, was selected for study (Bohart, Mezger, and Telford, 1953). From October 1, 1953, until November 1, 1954, daily temperatures and humidities at ground level were recorded by hygrothermograph. Tides and precipitation were also recorded. The marsh was visited every 7 to 10 days to tabulate the hatches and the relative abundance of the species. During each visit the salt concentrations of various tide pools were checked. Salinities were obtained by the use of a specific gravity hydrometer, previously calibrated to known salt concentrations at selected temperatures. This method was accurate within 0.1%.

Relative humidity of the macroclimate had comparatively little effect upon the marsh *Aedes*. The salinities of a day's samples were variable because of unequal evaporation rates from isolated pools. Extremes from less than 0.1% to 8.05% dissolved salt did not seem to affect the activities of these mosquitoes. Tides, rainfall, and temperature, however, did affect their conduct to a high degree. Figure 1 presents a weekly record of the highest tides and the highest rainfall in any 48-hour period. These are correlated with the hatches and relative abundance of the species. Figure 2 presents weekly high and low temperatures as they were related to the culicid populations on the marsh. The graphic use of extremes, in this case, illustrates the influence of temperature most clearly.

Preliminary investigations and earlier records (Bohart and Mezger, personal communication) indicated that the 1953–1954 observations at Bolinas were typical of the regular annual cycle. From these observations an analysis of a normal year of mosquito activity on the marsh can be made.

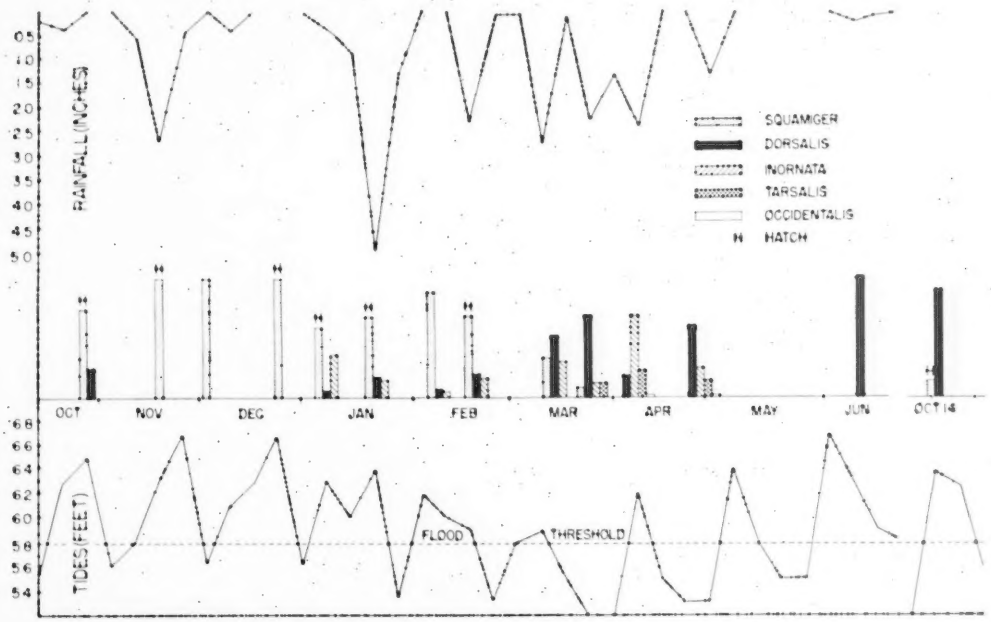

FIG. 1.—Highest weekly tides and highest weekly 48-hour rain totals as related to the hatches of *Aedes* and to the relative percentage of the species in larval populations on the Bolinas marsh from October, 1953, to October, 1954. *Note*: Tides and rainfall from July to October, 1954, are omitted because the marsh was occupied by *A. dorsalis* only during this period. Although there were no rains during these months, *A. dorsalis* produced a new brood with each flooding tide.

Bohart, Mezger, and Telford (1953) reported three main hatches of *A. squamiger* on the Bolinas marsh in 1952; each was preceded by heavy rains. Heavy rains and high tides from October, 1953, to February, 1954, permitted six distinct *A. squamiger* hatches (Figure 1). Development from hatching to the adult stage required approxi-

mately 48 days. Adult emergence occurred from February through March, reaching a peak in mid-March.

Quayle (1906) and Lowe (1932) reported numbers of *A. squamiger* adults on the marshes in the early spring. Very few adults were observed to remain on the Bolinas marsh in the spring of 1952, 1953, and 1954. However, they were abundant in the nearby foothills where they evidently had migrated immediately after emergence. An occasional female was taken on the marsh in late spring, weeks after the last adults had emerged.

Frequent attempts to observe *A. squamiger* mating gave no positive results. It is assumed that copulation took place in the wooded canyons nearby; many males and females were recovered from these areas in March and early April. In such canyons at twilight inaccessible swarms, believed to be mosquitoes, were seen 20 feet or more above the ground adjacent to eucalyptus and pine trees. During these observations *A. squamiger* females were persistently attempting to bite. *Culiseta inornata* (Williston), the only other mosquito in these areas, was not abundant and was observed swarming near ground level.

From March through April gravid females filtered back to the marsh to oviposit. Those remaining in the foothills were apparently killed by the first hot days of summer. A large population of females in a canyon at Black Point, Marin County, disappeared within 2 or 3 days in early July, 1953, and 1954, when the temperature exceeded 85° F. During this study males were never seen later than May.

In the spring, when the majority of the females oviposit, the lower areas of the Bolinas marsh are still under water. Only the higher, exposed portions are suitable for egg deposition at this time. Consequently, most *A. squamiger* eggs were located in higher areas where tides without a rain supplement could not reach them. By late spring, when the water receded, a few tardy females oviposited lower on the marsh. These late eggs hatched the following fall, when flooded by tides alone. Major hatches occurred as fall rains and high tides progressively flooded higher on the marsh. Although there is a series of hatches each year, a long developmental period and a summer dormancy of its eggs limit *A. squamiger* to one generation annually. Contrary to statements by Freeborn (1926), Lowe (1932), and Quayle (1906) this mosquito does not overwinter in the egg stage.

Regional culicidologists have repeatedly stated that brackish water produced by the first fall rains is required to stimulate an *A. squamiger* hatch each year. Figure 1 indicates that a rain of 0.5 inches preceded the initial *A. squamiger* hatch in 1953 (Oct. 28). This rain barely moistened the ground at Bolinas. However, tides exceeding six feet flooded a large portion of the marsh just prior to and during the time that first instar larvae were recovered. Figure 1 shows that the appearance of *A. squamiger* in 1954 (Oct. 14) was preceded by a 6.4 foot tide, but no rain. Salinities over the marsh at this time were 2.5‰. The first fall rains, therefore, can be discounted as the major stimulus initiating the annual hatch.

Field and laboratory investigations provided significant information concerning the summer dormancy of *A. squamiger* eggs and the stimuli required to hatch them (Telford, unpublished data). Flooding tides produced *A. squamiger* larvae in the fall and winter, yet, in the normal cycle, spring and summer tides did not effect a hatch. It is believed that aestivating eggs must be subjected to periods of low temperatures (below 45° F.) and perhaps a shortened photoperiod before they will hatch. Figure 2 shows that prior to the initial hatches in October of 1953 and 1954, the temperature had dropped to 42° F. and 40° F., respectively.

In the laboratory, environmental factors which were considered capable of stimulating *A. squamiger* eggs to hatch were experimentally eliminated until only temperature and photoperiod remained.[2] A positive correlation between the combination of temperature and photoperiod and hatching was indicated. However, these two factors could not be investigated independently because the necessary equipment was not available. The importance of photoperiod is questionable.

The aestivation period of these eggs then constitutes a true obligate diapause. The stimulus that initiates the diapause is intrinsic or hereditary in origin. Conversely, the stimulus that terminates it is extrinsic or environmental. Because diapause in *A. squamiger* is genetically induced, it is believed to be irreversible. Once it is broken, the individuals would not re-enter diapause but should remain ready to hatch when flooded. The following records indicate irreversibility of diapause in this species. Quayle (1906) believed that *A. squamiger* possibly had two generations annually because he observed a second adult emergence at San Francisco in September. Shanafelt (1950) reported *A. squamiger* adults at Huntington Beach on September 23, 1949. He found pupal cases and fourth instar larvae in a nearby area on the following day. Shanafelt added that the hatch followed an overflow of waste water on a reclaimed marsh.

A simple explanation might clarify the apparently similar observations of Quayle and

[2] *A. squamiger* eggs were subjected to hatching experiments involving exposure to various temperatures and temperature combinations during the development of the embryos, during storage subsequent to embryonic growth and at the time of flooding. Flooding media were also varied by altering the salinity and reducing the dissolved oxygen with infusions and chemicals. In addition, eggs were also exposed to variations of temperature and photo-period combined before inundation.

Shanafelt. Laboratory tests demonstrated that *A. squamiger* eggs remain alive without flooding for at least two seasons. After the irreversible diapause is broken, they should hatch when flooded. The area that produced the mosquitoes observed by Shanafelt had not been flooded for a year or more. Consequently, eggs persisting in the soil had been conditioned to hatch by low temperatures and (or) short daylight hours of a previous winter. Therefore, they hatched out-of-season when accidentally flooded.

Throughout the cold months of November and December, *A. squamiger* was the only mosquito inhabiting the Bolinas marsh. Among other factors, an irregular but progressive rise in temperature from January into the spring (Figure 2) enabled other mosquito larvae to occupy the marsh. A small hatch of *A. dorsalis* and a considerable hatch of *C. inornata* occurred during the second week in January. *A. dorsalis* became increasingly abundant until it was the only species on the marsh from June to October. Numbers of *C. inornata* fluctuated from January through April, when this species became dominant and then disappeared. *Culex tarsalis* Coquillett was not uncommon from late March into May in the higher pools. Larvae of *Anopheles occidentalis* Dyar and Knab were rarely recovered in April and May after *A. squamiger* had emerged.

Although Bolinas salinities did not deter the *Aedes*, they could be correlated with the occurrence of the other species. In late winter and spring the temperature rose, while heavy rains continued to dilute tidal water. *C. inornata*, a spring mosquito which is fairly tolerant of saline water, was recovered from pools ranging from 0.8% to 2.6% salt content. However, *C. tarsalis* was found only in pools of less than 1.0% salt.

Flooding tides and rainfall produced broods of *A. dorsalis* from January through October. In 1953, *A. dorsalis* had 12 broods and approximately 8 generations at Bolinas. During midsummer, it took about 12 days for a brood to mature. Most of the males emerged before the females. Swarming and mating took place on the marsh 1 or 2 days after emergence.

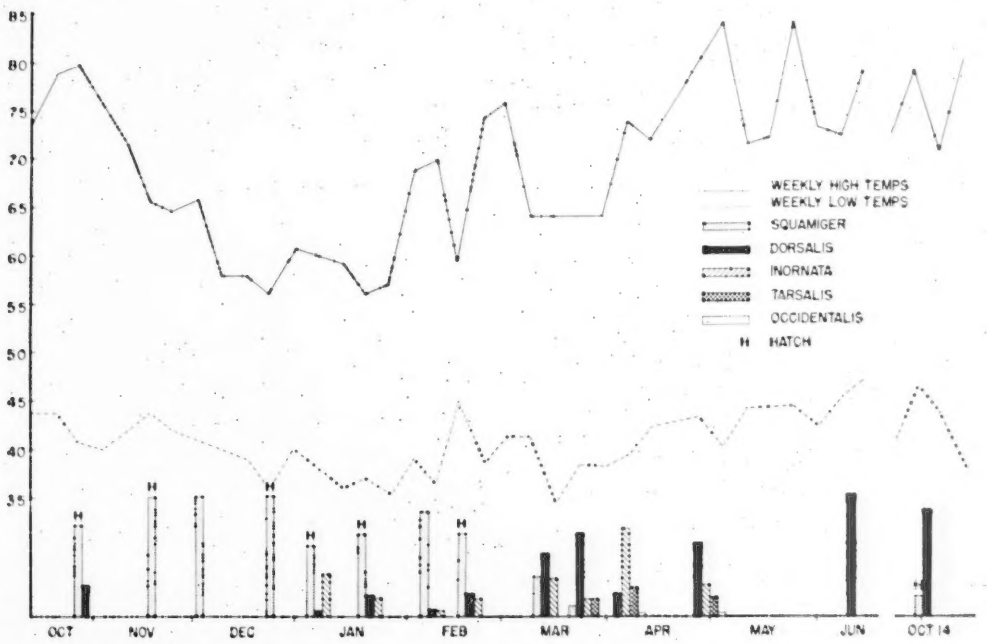

FIG. 2.—Highest and lowest weekly temperatures as related to the hatches of *Aedes* and to the relative percentage of the species in larval populations on the Bolinas marsh from October, 1953, to October, 1954. *Note.* Temperatures from July to October, 1954, are omitted because *A. dorsalis*, the only mosquito occupying the marsh during this period, continued to maintain itself at an optimum.

After mating, these mosquitoes dispersed from the emergence site. This random movement differs from the migration of *A. squamiger*. It is doubtful that an instinctive return flight to the original breeding area is involved. In spite of the natural dispersion, a great number of females remained to oviposit on the marsh. *A. dorsalis* was found on marshes throughout the summer except during dry periods of low tides. During the dry periods, they probably sought a more humid environment.

The last adults of the season emerged during

October. The females of this brood laid overwintering eggs and then died or were killed by the first frosts. Consequently, *A. dorsalis* was active for about 10 months of the year—January through October. The species was most abundant from late March to mid-October.

For 2 or 3 months of the winter (November-January), *A. dorsalis* as a whole hibernates in the egg stage. Laboratory data as well as field observations indicated that hibernation is probably a facultative diapause initiated primarily by the sharp temperature decline during this period (Figure 2). This diapause would differ from that of *A. squamiger* because it is not inherited but is induced by environmental factors. Only those eggs exposed to the rigors of cold are affected.

INLAND IRRIGATED PASTURE BREEDERS

In a natural environment *A. melanimon* and *A. nigromaculis*, California's inland pasture *Aedes*, would be limited to transient pools produced by the spring rains; however, in agricultural areas, populations perpetuate themselves due to intermittent irrigation. For the most part, then, these mosquitoes occupy an artificially produced habitat.

Observations during 1954 and 1955 indicated that in Yolo and Solano Counties few *Aedes* larvae appeared as a result of the first spring irrigations. However, with subsequent floodings they became abundant. Then there were as many broods as there were irrigations, up to a dozen or more in a single alfalfa field.

During the summer months field development normally varied from 6 to 10 days for these species. On rare occasions *A. nigromaculis* has been reported to complete its development in 3 to 4 days, but this has not been observed in Yolo and Solano Counties. When *A. melanimon* and *A. nigromaculis* occupied the same pool, *A. nigromaculis* matured 1 or 2 days earlier, the males of both species emerging before the females.

Within 48 hours of emergence, swarming and mating began at the emergence sites. On two occasions males of both species were taken from the same swarm. In spite of a natural dispersion, females were found at the breeding sites throughout the summer, provided a humid protective plant cover was available.

With the cessation of irrigation and the prevalence of lower temperatures (in late September and October) breeding was discontinued. After ovipositing, females of the last generation died or were killed by the first winter frosts. Winter rains did not hatch the eggs laid by females of this late generation.

It is suspected that *A. nigromaculis* eggs, like those of *A. dorsalis*, enter a facultative winter diapause. Here again temperature proved to be a major factor in conditioning eggs to hatch or remain dormant (Telford, unpublished data). *A. melanimon* is believed to act in a similar manner; however, difficulty of obtaining eggs prevented further confirmation with laboratory hatching experiments.

Warmer temperatures of the following spring then condition the eggs to hatch and initiate a new annual cycle. *A. melanimon* appeared approximately a month earlier than *A. nigromaculis* each year. This may indicate a greater tolerance for low temperatures by *A. melanimon*. It was commonly found from March into October while *A. nigromaculis*, on the other hand, was evident from mid-April into October.

Freeborn and Bohart (1951) stated that *A. nigromaculis* competed with fresh water *A. dorsalis* (*melanimon*)[3] and was rapidly replacing it in open sunlit pools. *A. nigromaculis* was said to have a competitive advantage because its eggs hatched within 2 to 6 days while those of *A. dorsalis* (*melanimon*) might be delayed for months.

Observations during 1955 indicated that *A. nigromaculis* and *A. melanimon* bred in the same general habitat, but that they occupied different niches. In mid-summer *A. nigromaculis* was found primarily in water that remained less than a week. All of 10 observed breeding sites of *A. melanimon* consisted of irrigation runoff which persisted for 2 weeks or longer. Furthermore, this species was never found in water that remained less than 5 days. *A. nigromaculis* was able to take advantage of evanescent water while *A. melanimon* evidently was not.

Laboratory experiments demonstrated that the embryos of both species reach maturity within 3 days at 80° F. When flooded in a suitable medium their eggs hatched within a few hours. Therefore *A. nigromaculis* does not have an advantage with respect to hatchability.

It is probable that the two species are not in direct competition. These data suggest that *A. nigromaculis* was introduced into an area where a suitable niche was widespread and unoccupied. It has so successfully occupied this niche that, locally, it now produces greater numbers than *A. melanimon*. As a result, the false impression arose that *A. nigromaculis* successfully competes with *A. melanimon*.

In central California *A. nigromaculis* in evanescent waters had no co-breeders. Occasionally, in deeper pools, it was found with *A. melanimon*. *A. melanimon*, in deeper runoff pools, was frequently associated with *Culex tarsalis* and *Culex stigmatosoma* Dyar. These *Culex* appeared in standing waters 2 days or more after *A. melanimon* larvae had hatched.

[3]Prior to the papers of Carpenter and LaCasse (1955) and Barr (1955) *A. melanimon* was regarded as a synonym of *A. dorsalis*. Previous references to *A. dorsalis* breeding in nonsaline water in the central valleys of California are now considered referable to *A. melanimon*.

ACKNOWLEDGEMENTS

I wish to thank Dr. R. M. Bohart, University of California at Davis, and Mr. E. G. Mezger, Solano County Mosquito Abatement District, for making available to me their notes and observations concerning the species treated in this paper and for their assistance during the investigation.

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OBSERVATIONS ON THE NESTING HABITS OF SOME NEW WORLD CARPENTER BEES WITH REMARKS ON THEIR IMPORTANCE IN THE PROBLEM OF SPECIES FORMATION

(HYMENOPTERA: APOIDEA)[1]

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ABSTRACT

The biological literature pertaining to the nesting habits of the New World carpenter bees belonging to the genus *Xylocopa* is organized and new biological information, particularly that relating to the nesting habits, is provided for eight American species. These are: *Xylocopa augusti* Lepeletier, *X. brasilianorum varipuncta* Patton, *X. californica arizonensis* Cresson, *X. frontalis* (Olivier), *X. guatemalensis* Cockerell (*X. pedens* Cockerell is declared a synonym), *X. micans* Lepeletier, *X. tabaniformis androleuca* Michener, and *X. virginica virginica* (Linnaeus). The importance of nesting habits in determining the probable ancestry, origin, dispersal and species formation in the group is discussed and evaluated. The accidental introduction of carpenter bees and their occasional successful establishment in new geographic areas is explored with the conclusion that care should be taken so as to prevent accidental introductions of species known to attack structural timbers.

Although more than one hundred species of the carpenter bee genus *Xylocopa* have been described from the Americas, suprisingly little is known of their biologies. The nesting habits of less than 30 species have been investigated, and those of only one, *Xylocopa virginica* (Linnaeus), are known in some detail (Rau 1933). Even though much of the information on the habits of our American species is fragmentary, nonetheless, its usefulness in connection with a revisionary study now in progress is already being realized. Unfortunately, many additional data are needed if an intelligent assessment of the New World *Xylocopa* fauna is to be achieved.

Malyshev (1931) has provided a convenient summary of the literature pertaining to the biology of the genus from a world viewpoint. The following references which provide additional information to that cited by Malyshev on the nesting habits of the New World *Xylocopa* have come to my attention: Bertoni 1918 (*X. artifex*, Paraguay); Blackburn and Kirby 1880 (*X. aeneipennis=brasilianorum sonorina*, Hawaii *cf.* Lieftinck 1956: 72); Burmeister 1876 (*X. augusti* and *X. frontalis*, Brazil); Cockerell 1914 (*X. libocedri=californica*, s. str., United States *cf.* Hurd 1955: 46); Howard 1893 (*X. virginica*, United States); Hurd 1954 (*X. californica* and its subspecies, United States); Hurd 1955 (*X. brasilianorum varipuncta*, *X. californica* and its subspecies, *X. tabaniformis* and its subspecies, and *X. virginica*, United States); Hurd 1956a (*X. rufina*, México); Hurd 1956b (*X. californica* and its subspecies, United States and México); Janvier 1955 (*X. eximia*, Perú); Ihering 1904 (*X. grisescens*, Brazil); Jorgensen 1912 (*X. brasilianorum* and *X. splendidula*, Argentina); Leach 1921 (*X. brasilianorum varipuncta* and *X. tabaniformis orpifex*, United States); Linsley 1943 (*X. tabaniformis orpifex*, United States); Moure 1942 (*X. artifex*, Brazil); Rau 1926, 1929, 1931, 1933 (*X. virginica*, United States); Ruiz 1940

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(*X. brasilianorum*, Chile); Schrottky 1902 (*X. bambusae*, Brazil); Schrottky 1904 (*X. augusti*, *X. colona*, *X. frontalis* and *X. splendidula*, Paraguay); Williams 1926 (*X. colona=darwini*, Galapagos Islands cf. Cockerell 1926: 659); Williams 1927 (*X. varipuncta=brasilianorum sonorina* Hawaii cf. Lieftinck, 1956: 72); and and Wolcott 1951 (*X. brasilianorum*, Puerto Rico).

In addition to the foregoing references there is a wealth of disconnected bio-ecological information in the voluminous literature which is in need of evaluation.

It is already apparent from a synthesis of the information on the nesting habits of the New World *Xylocopa* with the results of other investigations that a number of biological criteria bearing on the evolution of the group are emerging. This has placed a premium upon the acquisition of new biological information. Toward that end it is one of the objectives of this paper to focus on this fact by placing on record certain observations in the hope that these will stimulate research on the biologies of these bees.

The species of the genus *Xylocopa* appear chiefly to utilize a wide variety of dead, often systematically unrelated, plants or derived plant products in which to construct their nests. On rare occasions they are known to nest in living plants (Blair 1924), and not uncommonly in the dead parts of living plants. Some species select sound softwoods while others use sound hardwoods, or pithy, or hollow-stemmed plants, such as bamboo, *Arundo*, *Heracleum*, and *Merostachys*. Still others seem to prefer decaying or rotting woods. Then there are those which appear to be indiscriminate in their choice of a nesting substrate, but at least in some instances this appears to be more a consequence of the confused state of the systematics rather than the bee. In other apparently indiscriminate species I am led to believe that we are probably dealing with a species which is composed of a number of mosaic populations, each of which possesses a different trend in this respect. Additionally, predilection for a particular nesting substrate, though restrictive, does not preclude pioneering individuals and subsequently local populations from selecting nesting substrates new in character to the species as a whole. Rather, as is discussed elsewhere, it is believed that this process is essential to the initiation and development of new evolutionary trends.

A few species are known to nest as well in structural timbers and may become economically important. Thus in the United States three of the seven species (*X. californica*, *X. tabaniformis*, and *X. virginica*) nest rather consistently in structural timbers. Although, in general, the continued nesting within structural timbers causes little more than a great deal of noise and incidental damage (which probably is offset by their pollination of native and introduced plants), these bees may at times cause serious damage (Hurd 1955: 36). In view of this, precautions should be taken to prevent the possibility of introducing additional carpenter bee species which are known to attack structural timbers.

Inadvertent introductions have occurred a number of times in different places over the world. Possibly the best known is that of the Hawaiian *X. brasilianorum sonorina* Smith (Williams 1927), which in recent times also has become adventive in the Mariana Islands (Krombein 1950: 133) and has been intercepted in a shipment of wood at San Francisco, California (Hurd 1955: 35) and Japan (Maidl 1912: 264). Cockerell (1937: 111) states that *X. umbriata* Fabricius probably was introduced in the Barbados, being easily carried from South America with timber. Earlier, Cockerell (1912: 37) speculated on the possibility that his newly described subspecies, *Mesotrichia incerta seychellensis*, was of introduced origin and subsequently, treating the form as a species (Cockerell 1933: 2), remarked that there can now be but little doubt that the species was introduced in timber.

It would appear that accidental introductions, though not always successful, may occur more often than might be suspected. Indications that this is true continue to be suggested, not only by the above mentioned examples, but by a number of specimens which apparently were collected in adventive situations. Among the many thousands of New World carpenter bee specimens currently being studied, several are of particular interest in this connection. Two of these, a male of the Old World (India, China, Java, etc.) *Xylocopa* (*Platynopoda*) *latipes* (Drury) and a female of the Old World (India, Java, Siam, etc.) *X.* (*Nyctomelitta*) *tranquebarica* (Fabricius), are labeled: Colombia, S. A., Felipe Ovalle, Q. Ac. 33501 (American Museum of Natural History). Another female in the same collection, which I have not been able to identify satisfactorily to species, is a member of the widespread Old World subgenus (or genus) *Mesotrichia* Westwood. The specimen bears two labels which read: Port Castries, St. Lucia [West Indies] Ac 21,699 U.S.F.C. (U. S. National Museum). One additional record of some significance is that provided by two males of the North American *X.* (*Xylocopoides*) *californica diamesa* Hurd. These specimens are labeled: Ivon Beni, Bolivia, January, W. M. Mann, Mulford Biological Expedition, 1921–22 (U. S. National Museum). As has been explained elsewhere (Hurd 1955), the species *X. californica* (and its subspecies) are known to nest in structural redwood timbers and possibly may have been imported into Bolivia in this manner.

At present there is some assurance that the undescribed *Xylocopa* of Clarion Island (Revilla Gegedo Islands), located some 400 miles west of

the central Pacific Coast of México, is another example of an inadvertent and successful introduction by man. If this is so, the introduction has already resulted in a population which has diverged, phenotypically at least, from its putative continental progenitor.

Not infrequently man may introduce within or adjacent to the geographical range of a species acceptable nesting woods which are normally not available to the bees. These may be in the form of timbers or of plants which provide adequate nesting sites when dead or partly dead. Local range extensions of some species apparently result from the creation of these suitable nesting sites (Hurd 1955). Conversely, it is evident that destruction of nesting sites, however limited or extensive, will affect the geographic range or local distribution of a species. In Europe Haan (1952) and van Lith (1955) present evidence which shows that *Xylocopa violacea* (Linnaeus) is extending its distribution into areas previously not occupied by the species. It is probable that this has been brought about by an interplay of natural and man created factors.

As has been explained elsewhere (Hurd 1956b: 4-7), the probable evolutionary history of a species or even a higher category may be traced by a knowledge of nesting wood preferences of contemporary forms in light of the presumed floral histories involved.

The importance of nesting woods and their character in relation to the distribution and evolution of the group seems inescapable. It therefore appears highly desirable to preserve this information so that it may be considered in terms of other features.

It should be noted that a few Palaearctic species, formerly included in the genus, were shown to nest in the ground by Malyshev (1913) and Gutbier (1914, 1916). This provided a basis for a morphological re-evaluation which has more properly placed these species as a primitive xylocopine genus *Proxylocopa* Hedicke (Maa 1954), whose composite structures and biologies would appear to me to favor an anthophoroid origin for *Xylocopa* in the broad sense. The wood nesting *Anthophora* (*Clisodon*) *furcata* (Panzer), unlike its congeners that nest in the ground, appears to be a parallel example favoring this view.

Malyshev (1913) has postulated that the carpenter bees (*Ceratina* and *Xylocopa*) had a common, but unstated, ancestor whose branched nests were constructed in dry and compacted

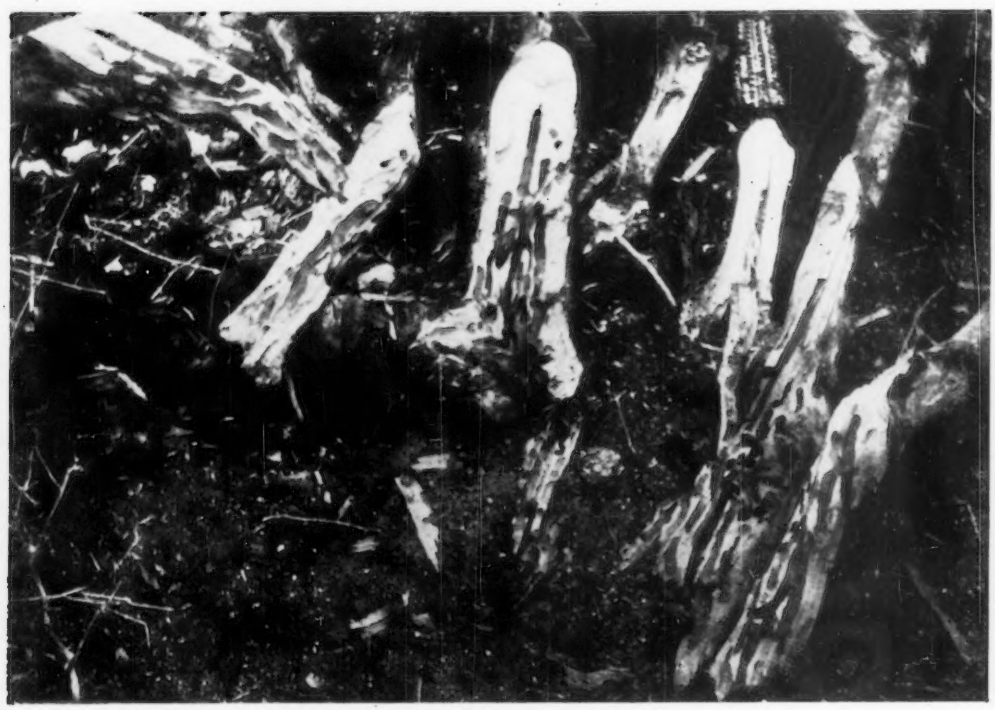

FIG. 1.—Nest of *Xylocopa brasilianorum varipuncta* Patton in the base of an organ-pipe cactus, *Cereus thurberi*. (Photograph, courtesy of R. E. Ryckman).

soil. This ancestral stock, according to his hypothesis, was more like the contemporary ground-nesting carpenter bees of Turkestan (*Proxylocopa*) than the modern wood-nesting carpenter bees (*Ceratina*, *Xylocopa*, etc.). These latter genera he believes were evolved from the ancestral stock through the abandonment of the undergound nests in favor of half-decayed wood. In this habitat the evolving line, however, was confronted by the problems, such as molds, resulting from long periods of rain, cold, and humidity. Moreover, the bees had no special means, such as cocoons and water impermeable cell linings, to cope efficiently with this environment. To overcome these difficulties partly,

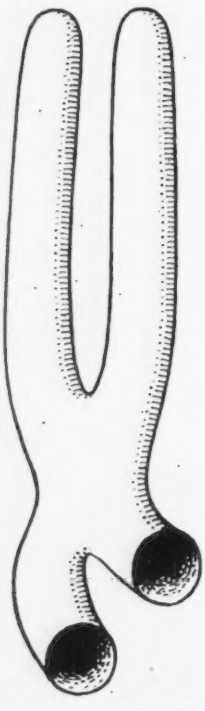

FIG. 2.—Diagram of the nest of *Xylocopa frontalis* (Olivier) in a hardwood fence post.

Malyshev reasons that in the autumn the young transformed into adults (abbreviating diapause and lengthening adult life) and left the nest to seek dry shelter for the ensuing winter (hibernation). In an attempt to alleviate further the difficulties inherent in the decaying wood habitat some of the bees commenced nesting in drier and harder wood. At this point two principal evolutionary lines were initiated, according to Malyshev. One of these, which has led to the modern *Ceratina*, selected small pithy stems, a consequence which has evolved a group of small bees whose nests have lost through mechanical limitation the more primitive branching characteristics. The other line eventually led to the formation of larger species (greater choice and diversity of dry-wood nesting substrates) and has today culminated in the modern *Xylocopa* which retain traces of the more primitive branched nest (as in fig. 3).

An interesting aspect of this hypothesis is the inherent suggestion of the climatic (contrasting seasons) and floral (proximity of woody plants) conditions in which the group appears to have evolved. If this is so, then the origin of the carpenter bees most likely occurred in or adjacent to a montane temperate forest. The presence today of the more primitive ground-nesting genus *Proxylocopa* in Eurasia suggests that these events took place in the northern hemisphere. The invasion of the new habitat (plants) and its great ecological diversity could have provided the necessary avenues of geographical dispersal that have led to subsequent radiation and proliferation of the great number of species living today in the tropics of the world.

None of the American species are known to nest in the ground, although Hubbard (in Howard 1893: 332) has reported "their burrows in a kind of 'hard pan' or soft sandstone which was used in lieu of brick in the construction of greenhouses, . . . and in one instance a supporting pier was honeycombed and undermined by these creatures." These observations were made at Crescent City, Florida, on *X. virginica* (Linnaeus), a species which normally nests in sound wood.

Judging from the morphological characteristics of *X. serripes* Burmeister (1876: 156), which was described on the basis of a male and female from Rio de Janeiro, Brazil, it may be that this species nests in the ground. According to Padre Moure (*in litt.*) there is a likelihood, however, that the specimens upon which Burmeister founded his description may have been of introduced origin.

I am grateful to Drs. C. D. Michener, University of Kansas, Lawrence; T. B. Mitchell, University of North Carolina, Raleigh; Padre J. S. Moure, University of Paraná, Curitiba, Brazil; H. J. Reinhard, Texas A. & M., College Station; R. E. Ryckman, College of Medical Evangelists, Loma Linda, California; and T. E. Snyder, U. S. National Museum, Washington D. C., for placing their original observations at my disposal. My thanks are also due to P. H. Timberlake, University of California, Riverside, and J. A. Powell and Gerald I. Stage, University of California, Berkeley, for their observational assistance at the Surprise Canyon locality.

Celeste Green, Scientific Illustrator, Department of Entomology and Parasitology, University of California, Berkeley, kindly prepared the diagrams (figs. 2 and 3) from field sketches loaned by Dr. Michener.

Xylocopa augusti Lepeletier

Dr. C. D. Michener and Padre J. S. Moure observed this species nesting in sound, unhewn, hardwood fence posts at Araucaria, Paraná, Brazil, on January 13, 1956. One of the nests, which was composed of several branches, contained adult bees (two males and a number of females) and two larvae, one half-grown, the other mature. Several cells had "pollen masses (eggs inside?)." Many of the cells contained larvae and pupae of an undetermined bombyliid. Another nest studied by them had "only one female bee, no pupae, two mature larvae and two pollen masses (eggs inside?)."

Previous information on the nesting habits of this species suggest that it prefers sound hardwood, including structural timbers, for nesting.

Xylocopa brasilianorum varipuncta Patton

The males of this subspecies, as observed by Dr. Michener in California, as well as those of similar species studied by him in Brazil, México, and Panamá, fly about within the branches and foliage of a selected tree or group of bushes for hours at a time. The purpose of the flight, he speculates, may be related to mating in some way. He has found that the same male returns to the same place day after day and when one of these males is caught, none replaces it, whereas previously it had been buzzing about and among the branches of the same tree for a week or two. A somewhat similar behavior has been noted for the males of the Old World subgenus *Coptorthosoma* (= *Maiella*) by Lieftinck (1957: 326).

Unlike its Hawaiian counterpart, *X. brasilianorum sonorina* Smith, with which it has been synonymized (Timberlake 1922: 51; Lieftinck 1956: 72) and which seems to prefer to nest in sound wood including structural timbers (Williams 1927: 429–432), the subspecies *varipuncta* of the southwestern United States and northwestern México appears to utilize only rotting or decaying wood (Hurd 1955: 36).

During the past summer, July 15, 1957, this subspecies was found nesting by Raymond E. Ryckman, his sons, Albert and Joseph, and Dean Spencer, in a large dead organ pipe cactus, *Cereus thurberi* (det. Annetta Carter, University of California Herbarium) some 2 miles north of Cabo San Lucas, Baja California, México. The burrow entrance, from which several burrows radiated (fig. 1), was located at the base of the cactus about 1 foot above the ground on the eastward, downhill slope exposure. When the cactus was split open some 50 to 100 bees of both sexes escaped, of which 29 were collected including an unexplained female specimen of another species *X. tabaniformis androlenca* Michener. It is thought, however, this bee may have been either resting within some other part of the cactus or may have been attracted by the commotion. The harassed bees, though they flew confusedly about after returning to the disturbed nesting site, did not aggressively defend the nest. Within the nest a number of larvae (young, half-grown, and mature), pupae, and several pollen masses were found. No eggs were in evidence.

Xylocopa californica arizonensis Cresson

During the California Insect Survey spring trip of 1957 to Surprise Canyon, Panamint

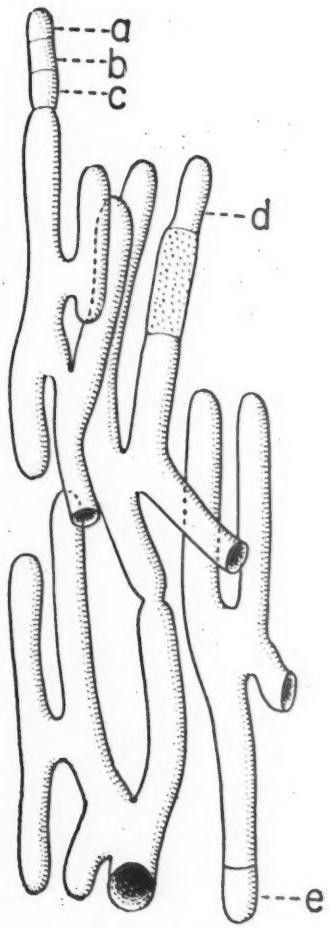

FIG. 3.—Diagram of a group of nests of *Xylocopa frontalis* (Olivier) in a hardwood fence post. (See text for details).

Mountains, Inyo County, California, the nesting activities of this subspecies were under observation for several days (April 20–26). As reported elsewhere (Hurd 1956: 6), *arizonensis* at this locality has accepted and is nesting in timbers of coast redwood, *Sequoia sempervirens*, which except

for the intervention of man would not be available to the bee. It would appear that the subspecies nests normally in various interior yuccas and agaves (Hurd 1954).

Here *arizonensis* occurs together with another carpenter bee, *X. tabaniformis androleuca* Michener which belongs to another subgenus. This latter species nests in a different wood (Douglas fir, *Pseudotsuga taxifolia*), but in the same buildings being used by *arizonensis*. As explained in the account of *androleuca*, that bee has a much different daily activity pattern.

X. californica arizonensis already had commenced nesting activity and nest construction was well underway. Active nests, all constructed in redwood, were located in roof rafters and sheathing, building sidings and sills, floor joists and planks, door and window frames, porch railings and even table legs. Invariably the burrow entrances were located on the most protected exposure. Those burrows situated in vertical or slanting timbers turned upward following the grain from the entrance, while those in horizontal timbers extended laterally with the

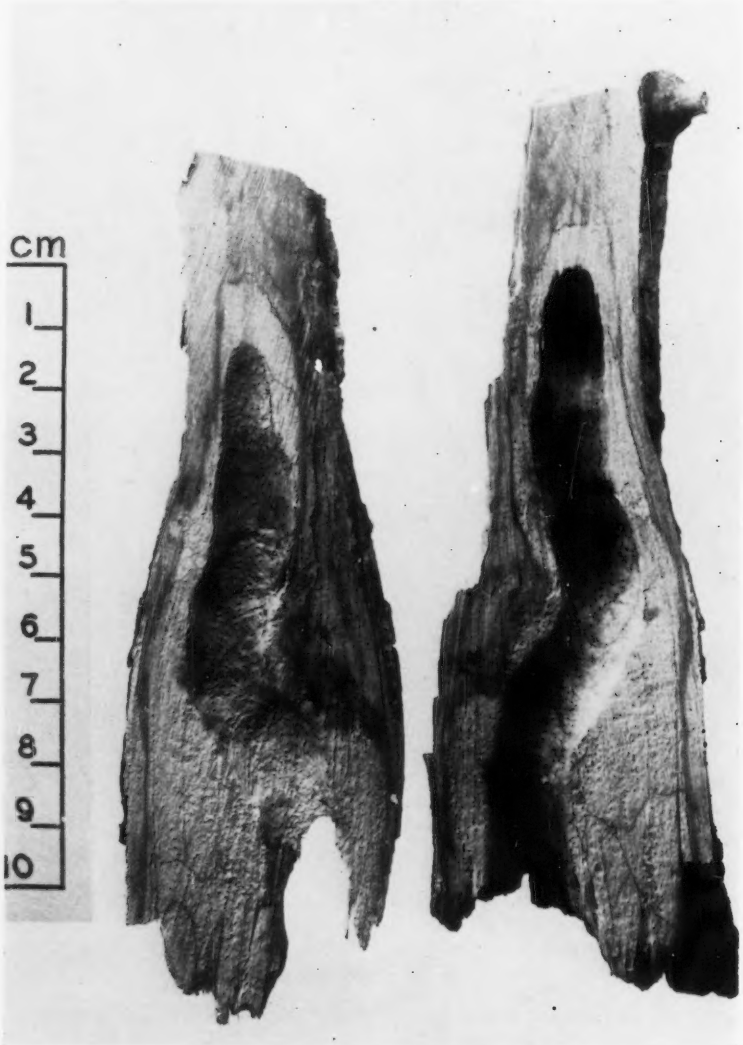

FIG. 4. Counterpart longitudinal sections of the nest of *Xylocopa micans* Lepeletier in a dead privet hedge stem, *Ligustrum*.

grain from the entrance which most often opened on the lower or ground facing surface though in some instances opened on the very narrow vertical surface. One section of roof sheathing boards running along the eaves, when split open, revealed that each board, some twelve inches wide and five-eighths inches thick, was almost completely channeled by a series of longitudinal tunnels, often interconnected, and sometimes almost six feet in length. Quite obviously a good many years of tunneling by many generations of bees had been involved. One of the current season's burrows contained three newly cut cells but without pollen stores. Owing to the location of other active nests it was impossible to investigate without doing considerable damage to the buildings. It was apparent, however, from the pollen-laden females entering other burrows that provisioning had begun. As near as could be determined the only pollen source being utilized by the females was the creosote bush, *Larrea glutinosa*, although some females were observed on the flowers of *Stanleya pinnata*, but were apparently only in quest of nectar.

The daily activity pattern of this bee is discussed in the account of *X. tabaniformis androleuca*.

During the warmer part of the day the pollen-laden females returning to their burrows were confronted a short distance from the buildings by a large number of hovering, audibly buzzing males. The female, apparently attempting to avoid contact with the males, would fly directly toward her burrow entrance, passing beneath the hovering males. Frequently several males would pounce upon her whereupon a brief struggle would ensue in which one of the males would apparently successfully copulate with her. The united pair would circle together for several seconds in mid-air and separate almost invariably at several feet above the level of their initial union. Upon separation the female would fly directly to her burrow and the male would return to the hovering flight. The longest union observed lasted 30 seconds, with the pair flying together and alighting among the foliage near the top of a nearby cottonwood tree. Not infrequently the copulating pair would be subjected to the aggressive attentions of other males, but this served no other purpose than to drive the united pair away from the immediate vicinity. At times the struggle of several males for a returning female would become so intense that the female would escape the attention of the embattled males and fly directly to her burrow. No attempt was made by the hovering males to pursue a female leaving her burrow, possibly because her rapid flight was unexpected and direct.

The hovering flight of males persisted for about 1 hour (about 1 to 2 p. m. P.D.T.), toward the end of which most of the males had left in search of nectar even though the females continued pollen provisioning well into the late afternoon hours before returning to their respective burrows for the night. On the basis of these observations the males of *arizonensis*, unlike those of such species as the Old World *X. aestuans* (Linneaus), in which both sexes engage in nest construction (Blair 1924), appear not to assist the female. At night the males gather together in close proximity of each other within the old burrows. Their daytime activities center largely about obtaining nectar for their own purposes and mating with the females.

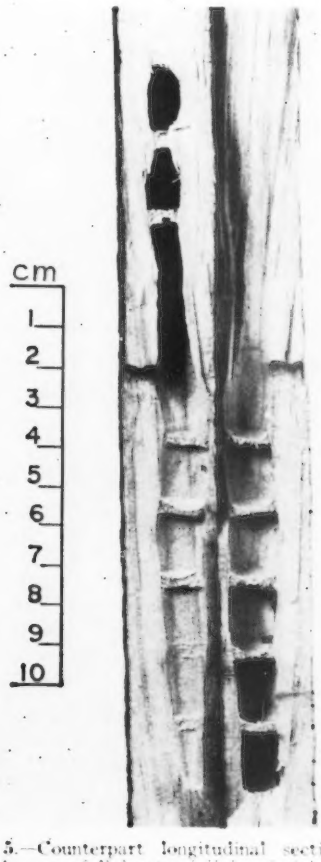

FIG. 5.—Counterpart longitudinal sections of the nesting burrow of *Xylocopa virginica virginica* (Linnaeus) in a white pine board, *Pinus strobus*.

Xylocopa frontalis (Olivier)

Schrottky (1904: 347) has remarked on the species, penchant for fence posts, tree stumps and the like, but notes interestingly that it fails to avail itself of structural timbers of houses. Of further interest is the fact that one of its nearest relatives, *Xylocopa fimbriata* Fabricius, appears to utilize any dry decaying wood for nesting purposes (Bodkin 1918: 209).

This species, which is one of the largest of the New World, was observed by Dr. C. D. Michener and Padre J. S. Moure at Caiubá, Paraná, Brazil on February 2, 1956, nesting in unhewn, sound, hardwood fence posts. One of the nests (fig. 2) studied by them was situated near the ground with a double entrance, each entrance measuring approximately 23 mm. in diameter. A burrow from each entrance led inward and upward for a short distance, briefly interconnecting, then separating and continuing upward as two separate tunnels. The overall length of the nest was 21 centimeters with the upper tunnel diameters measuring 19 mm. (left) and 20 mm. (right). No cells or partitions had been made. Two female bees were captured in the nest.

Another fence post investigated by them contained a group of nests with several entrances located between 6 and 30 centimeters above the ground (fig. 3). Many bees of both sexes escaped and disappeared, but later returned with the females aggressively flying directly toward the intruder. In this connection, Bertoni and Schrottky (1909: 40–42) found this species to be extraordinarily irritable, aggressive in character, and display much "bravery" in the defense of their nest. These authors cite the example of a wood cutter, who at the end of summer, sinks his axe into an old tree trunk only to be attacked about the head by ". . . sixteen, including the mother, raging, buzzing black [females] and yellow [males] devils . . ."

The uppermost nest (fig. 3) contained three cells (a, b, c,) which in descending order had a male pupa, a recently emerged female (unpigmented wings), and a female pupa. In the lower right nest (fig. 3e) a dead pupa was found in a partitioned cell at the bottom of the lowermost burrow. One of the terminal cells in the nest series had a diameter of 20 mm. and measured 22 mm. in length from the inner surface of the cell partition to the extreme apex. A larva of the meloid genus *Cissites* was found in the upper terminal cell (fig. 3d). A sawdust plug (indicated by stipple) sealed the cell from below. Strand (1912: 264) has illustrated a similar plug made by the meloid in a terminal cell of the nest of *Xylocopa nigrocincta* Smith.

The association of the meloid genus *Cissites* with *Xylocopa* has been reported several times from the New World, but almost invariably the beetle has been determined as *Horia maculata* (Swederus). MacSwain (1956: 107) remarks that although the genus *Cissites* is similar in many respects to the genus *Horia*, it would appear that *Cissites* is the more recent and specialized group. The genus *Cissites*, according to him, contains the larger number of species and is essentially pantropical in distribution, though absent from Australia, while *Horia* is restricted to the Old World tropics including Australia.

In the New World, larvae of the genus *Cissites* have been recorded in the nests of three species of *Xylocopa*, *X. teredo* Guilding from the West Indies by Guilding (1824: 315), *X. augusti* Lepeletier from Brazil by Burmeister (1876: 154), and *X. nigrocincta* Smith from Paraguay by Strand (1912: 263). Dr. J. W. MacSwain informs me that the meloid identified by Guilding as *Horia maculata* is probably *Cissites auriculata* (Champion) and that those similarly determined by Burmeister and Strand are most likely *Cissites maculata* (Swederus).

Triungulin larvae of the meloid genus *Cissites* have been reported clinging to the body hairs of adult New World *Xylocopa* by Brues (1924: 125) and MacSwain (1956: 108). The triungulins recorded and illustrated by Brues and identified by him as *Horia maculata* (Swederus) = *Cissites* (MacSwain, *in litt.*) were taken from a female bee which had been collected on South Seymour Island, Galapagos Islands. The *Xylocopa* of these islands has been variously identified as *X. brasilianorum* (Linnaeus) by Maidl (1912: 312), *X. transitoria* Pérez by Brues (1924: 125), and *X. colona* Lepeletier by Rohwer (1924: 173) and Williams (1926: 348, 356). Subsequently it has been regarded as an endemic species, *X. darwini* Cockerell (1926: 659, 1935: 379) and Cheesman (1929: 143). The *Cissites auriculata* (Champion) triungulins studied by MacSwain (1956: 108) were removed from a male specimen of an undetermined *Xylocopa* collected by E. G. Smyth at Cuernavaca, México on November 4, 1922 (U. S. National Museum). I have examined this specimen and find it to be *Xylocopa guatemalensis* Cockerell, a Central American species which belongs to the subgenus *Notoxylocopa*.

Xylocopa guatemalensis Cockerell

Males of this species, which were described by Cockerell (1949: 483) as *X. pelëni* (new synonymy, Hurd & Moure), were observed in hovering flight during the early forenoon hours (9 a.m. to 10:30 a.m.) along a mountain trail between San José Inapila and Aurora in Chiapas, México on February 2, 1956.[2] The males hovered almost noiselessly in the warm sunshine singly or in small groups along and adjacent to the trail some 6 to 8 feet above the ground in an area predominated by dead *Dahlia* stalks. When disturbed by collecting attempts they would rise in hovering flight, often erratically moving about the higher reaches of the vegetation. No females were observed and nothing is known of their nesting habits.

Lieftinck (1955: 24–25) has observed males of the Old World *Xylocopa perversa coracina* Van der Vecht in the hills of West Java behaving somewhat similarly. He notes that a high-pitched

[2]These observations were made in the course of an expedition sponsored by the Associates in Tropical Biogeography, University of California.

shrill buzzing sound is made on any sunny day during their hovering flights which occur in sunlit openings, among isolated plots of trees and shrubbery on the hill slopes, or beside streams in wooded country between 8 a.m. and 10 a.m. He reports that on hot days all males disappear suddenly about the middle of the morning and occasionally reappear late in the afternoon, but if rain falls early in the morning the flight commences much later.

Xylocopa micans Lepeletier

The nesting habits of this, the type species of the subgenus *Schönherria*, have been unknown, excepting a cryptically labeled specimen taken "from a nest in stick" in July, 1912, at Billy's Island, Okefenokee Swamp, Georgia (Hurd 1955: 63).

During a recent visit with Professor H. J. Reinhard, he recalled that he had observed in past years the nesting of a *Xylocopa* in the dead parts of his privet hedge (*Ligustrum*) at College Station, Texas. It was not long thereafter that I received the nest shown in figure 4 containing a dead female of this species. Professor Reinhard writes that the carpenter bee was nesting in the privet hedge about 3½ feet above the ground with the burrow entrance facing southeastwardly. He remarks that he has seen other nest entrances closer to the ground, in fact, on one occasion the nest under observation was barely 6 inches above the ground with the entrance facing slightly west of south. The stem selected for nesting, he writes, was dead but sound with a diameter of one or more inches.

Xylocopa tabaniformis tabaniformis Smith

In the collections of the U. S. National Museum there is a female of this subspecies labeled: San Pabo de Tarrazu, Costa Rica, February 11, 1937, in dead coffee trunk, C. H. Ballou and A. Chévez. This record constitutes the first information on its nesting activities.

Xylocopa tabaniformis androleuca Michener

This subspecies, which was found nesting in a Douglas fir (*Pseudotsuga taxifolia*) porch studding of a cabin in Surprise Canyon, Panamint Mountains, Inyo County, California (Hurd 1955: 58–59, table 1), was observed again at the same locality between April 20 and 26, 1957, during a California Insect Survey spring trip. The normal nesting wood selected by this bee is unknown, but there is reason to believe that juniper may be involved.[3] Nesting activities had not commenced, but three or four males and females were noted during the sunny early morning hours (6 to 9 a. m., P.D.T.) in quest of nectar at the flowers of *Larrea glutinosa* (females) and *Stanleya pinnata* (males). No other *androleuca* were seen until mid-afternoon, when a few males were observed by Powell at the flowers of *Stanleya*. This was in marked contrast to the activity pattern of the much larger carpenter bee, *Xylocopa californica arizonensis* Cresson, which also nests here, but uses the coast redwood structural timbers. Nesting of this latter bee was already underway but its daily activity period was confined chiefly to the warmer daylight hours. The first bees appeared in the morning (after the activities of *androleuca* had ceased) continued with increasing abundance into the warmest part of the day (shortly after 2 p. m. P.D.T.) and decreased during the later afternoon hours until all but a few stragglers had retreated to their burrows for the night. All activity on the part of *arizonensis*, including the settling buzzing noises within their tunnels, had ceased by sunset. At dusk the first buzzing noises of the main flight of *androleuca*, easily detected by a different pitch, commenced. Soon the males began to depart singly from their congregations within the old abandoned burrows of *X. californica arizonensis* where they had spent most of the daylight hours. The females of *androleuca*, which had rested singly within the old burrows of their own race, appeared shortly after the males began leaving their resting tunnels. Both sexes flew off into the gathering darkness, but it was not learned for what purpose. Repeated observations of the possible nectar sources adjacent to the buildings failed to demonstrate the bees. The evening activity of *androleuca* had ceased some 2 hours after dusk, following the return of the bees to their respective quarters. None of the collected females exhibited even a trace of pollen on their scopa. The period of greatest activity for *androleuca* on the basis of these observations would appear to be the evening hours.

During the day the males could easily be collected by striking the net handle against the board containing the tunnels of resting males and capturing them as they left the tunnel entrance in confusion.

Xylocopa virginica virginica (Linnaeus)

The investigations of Rau (1933) on the biology of this bee have provided us with the most complete account for any New World species of the genus. This subspecies prefers to construct its burrows in the dead sound wood of a variety of different plants frequently including structural timbers in which they sometimes occasion some damage.

On my recent visit to the U. S. National Museum, T. E. Snyder informed me that he has observed the bee in Washington, D. C., nesting a number of times in the structural timbers of Bald Cypress, *Taxodium distichum*, Southern yellow Pine, *Pinus palustris*, and White Pine,

[3]Snyder (1927) has figured the burrow of an undetermined *Xylocopa* in juniper which he tells me was taken in Sabino Canyon, Arizona, in 1916.

Pinus strobus. In Kansas, Dr. C. D. Michener located in 1956 a nest in a dead branch of a living Northern Red Cedar, *Juniperus virginiana*, some 6 miles south of Lawrence. The burrow entrance was situated on the underside of an upward sloping branch some ten feet above the ground.

Dr. T. B. Mitchell kindly furnished the nest shown in figure 5, which was made in structural white pine. It was collected by Mr. John Flynn in Clayton, Johnston Co., North Carolina. Dr. Mitchell writes that these bees are giving Dr. R. L. Rabb some trouble since they are nesting in the shelters he has made of white pine for some experiments in the use of *Polistes* for the control of tobacco horn worms.

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NORTH AMERICAN MAYFLIES OF THE FAMILY OLIGONEURIIDAE[1]

GEORGE F. EDMUNDS, JR.,[2] LEWIS BERNER,[3] AND JAY R. TRAVER[4]

ABSTRACT

Present knowledge of the family in this continent is reviewed, and a key is given to its two North American genera, both as nymphs and as adults. Males from Kansas are described as probable adults of *Homoeoneuria ammophila* (Spieth), originally described in *Oligoneuria* from nymphs taken in Indiana and later found also in Illinois. Adults and nymphs of *H. dolani*, n. sp., are described from Georgia and South Carolina, chiefly from the Savannah River. *Homoeoneuria* nymphs, unassociated with adults and not identifiable to species, have been collected in Florida, Mississippi, Texas, and Nebraska. The genus was first known from Guatemala. In its body form and legs the nymph strongly resembles the Russian genus *Oligoneuriscus*, but its distinct nature and the unique absence of forceps indicate that *Homoeoneuria* occupies an isolated position within the family. The nymphs are inhabitants of larger streams, where they live buried in the shifting sand bottom; some observations on their activities are included. Adults emerge from early June through late October. *Lachlania saskatchewanensis* Ide and *L. powelli* Edmunds, the other North American representatives of the Oligoneuriidae, are briefly discussed.

At the time of Traver's (1935) revision of the North American mayfly fauna, the family Oligoneuriidae was not known from North America north of Mexico. In the present paper we record two genera and several species from ten states and one Canadian province. The members of this family are easily identified in both nymphal and adult stages. The adults are readily recognizable by the unique wings in which cross venation is greatly reduced or absent, intercalary veins are reduced or absent, and the concave veins are hidden beneath the convex veins to give the appearance of a greatly simplified wing (figs. 10 and 30). The males are unusual in that the fore legs (fig. 7) are *shorter* than the middle or hind legs (figs. 5 and 6). The nymphs (figs. 15 and 31) resemble *Isonychia* (Siphlonuridae: Isonychiinae) in having long setae on the femur and tibia of each fore leg, but may be immediately distinguished by the much smaller gills on segments two to seven, and by the ventral position of the gills on segment one. The North American genera of Oligoneuriidae may be distinguished by the following key.

1. Adult 2
   Nymph 3
2. Terminal filament present and as well developed as the cerci; veins R_3+IR_3 not present in forewing, thus the wing has only three apparent longitudinal veins in the disc (fig. 10); male lacking genital forceps (fig. 4) ..... **Homoeoneuria** Eaton
   Terminal filament lacking, only the two cerci present; veins R_3+IR_3 present in forewing, thus the wing has four apparent veins in the disc (fig. 30); males with genital forceps ..... **Lachlania** Hagen
3. Lamellate portion of gills on segments two to seven oval, fibrilliform portion well developed; ventral first gill similar to others; coxae of metathoracic legs much smaller than femora (fig. 31) ..... **Lachlania**
   Lamellate portion of gill on segments two to seven lanceolate, fibrilliform portion wanting (figs. 24 and 25); ventral fibrilliform portion of first gill greatly enlarged (fig. 23); coxae of metathoracic legs larger than femora (fig. 29) ..... **Homoeoneuria**

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Genus **Homoeoneuria** Eaton

The genus *Homoeoneuria* was described by Eaton (1881) from females of *H. salviniae* collected at Dueñas (4950 feet elevation), and at Aceytuno (5100 feet elevation), Guatemala. Subsequently Eaton (1892) added some notes, but the genus remained unmentioned for many years.

Spieth (1937) reported an unusual oligoneurid nymph from the White River at Decker, Indiana, the first record of the family in North America. After he collected additional specimens he named this form *Oligoneuria ammophila* (1938). Burks (1953) reported the same species in Illinois.

In the summer of 1951, Edmunds secured two cast skins of nymphs at Kearney, Nebraska, that were very similar to *Oligoneuria ammophila*. From raised ridges on the wing pads of these nymphal exuviae it was possible to reconstruct the very characteristic wing venation of the genus and the unique absence of forceps, it would appear that *Homoeoneuria* occupies an isolated position within the Oligoneuriidae. The absence of the forceps is not due to their loss in preserved material, for they are missing from all our specimens and the developing genitalia of the nymph also confirm their complete absence.

The absence of genital forceps (fig. 4) and the shape of the hind legs, with their strongly bowed coxae and femora (fig. 5), indicate that the female must be held by these legs during mating. Further, the presence of short, coarse, curved spines on the inner surfaces of the femur and tibia provide additional support for this conclusion. It is likely that the legs are swung dorsally so that the femora can embrace the female abdomen, and at the same time the spines of the femora and tibiae prevent slipping. The large, bulb-like claws (fig. 8) with their pubescent surface also may assist in holding the

FIG. 1. The Homochitto River, Mississippi, at June, 1956, level showing exposed sand bed. That part of the bed covered with water was similar to the exposed portion.

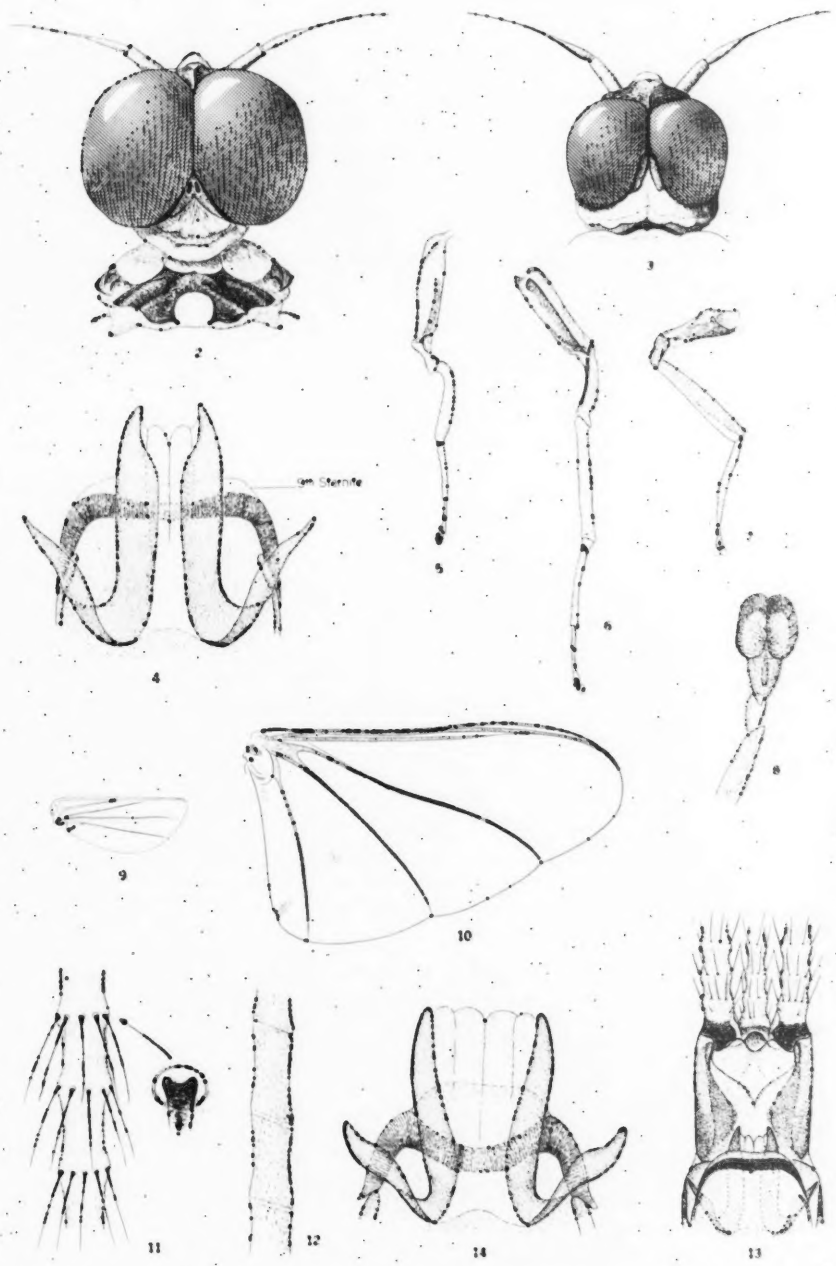
Homoeoneuria, and *ammophila* was subsequently transferred to that genus by Edmunds and Allen (1957: 318).

In the summer and fall of 1951, while surveying the Savannah River in Georgia and South Carolina, Thomas Dolan IV and Selwyn S. Roback collected a number of adults of this genus from the surface of the river's waters and also collected nymphs from the river. Since 1951, nymphs or adults of *Homoeoneuria* have been collected also from various localities in Georgia, South Carolina, Florida, Mississippi, Texas, and Kansas.

Because of the distinct nature of the nymph mating insects together as they do in *Lachlania*.

The wing venation of *Homoeoneuria* (fig. 10) is the most reduced of any in the order but is most similar to that of *Elassoneuria*, the two sharing the feature of the absence of R_3 and IR_3. The nymph of *Elassoneuria* (Lestage 1916, and Ulmer 1920) is quite unlike that of *Homoeoneuria*, with little suggestion that *Homoeoneuria* and *Elassoneuria* are closely related.

The nymph of the Russian genus *Oligoneurisca* bears a great resemblance in body form and legs to that of *Homoeoneuria*, and may be closely related, although the similarity might be a result of convergent evolution. The incipient wing



FIGS. 2 to 13.—*Homoeneuria dolani*, imago paratypes.

FIG. 2.—Head and prothorax of male, dorsal view.
FIG. 3.—Head of female, dorsal view.
FIG. 4.—Male genitalia, dorsal view.
FIG. 5.—Male metathoracic leg.
FIG. 6.—Male mesothoracic leg.
FIG. 7.—Male prothoracic leg.
FIG. 8.—Detail of prothoracic claw of male.
FIG. 9.—Male metathoracic wing.
FIG. 10.—Male mesothoracic wing.
FIG. 11.—Detail of male cercus.
FIG. 12.—Detail of female cercus.
FIG. 13.—Male terminalia, ventral view.

FIG. 14.—*Homoeneuria ammophila* (Spieth)?, male genitalia, dorsal view.

venation is reminiscent of *Oligoneuriella*, but if the first two apparent veins in Tshernova's (1937) drawing are actually C and R_1, then the wing venation would be very similar to that of *Homoeoneuria*. Although this is possible, it does not appear likely; an adequate knowledge of the venation will have to await adults of *Oligoneurisca* and a more thorough study of all the genera in the family.

The taxonomic relations within this genus are difficult because of the fragmentary nature of most collections. We are able to distinguish two species of adults which are recognizable only on the basis of minor differences in color and the male genitalia. After careful examination of nymphs from all localities, we have been unable to find any characteristics for separating them.

Even though we are unable to distinguish the nymphal forms, we feel that it is best to consider the Savannah River forms as being a separate species. It is probable that the males which we have from Kansas represent the adults of *H. ammophila* Spieth, and these are certainly not conspecific with the Savannah River specimens.

Homoeoneuria dolani, new species

Male imago.—Length: body 8–9; wing 6–7; terminal filament and cerci 7–8 mm. *Head:* Dark brown; eyes dark brown, contiguous dorsally (fig. 2); antennae placed very near the nasal carina. *Thorax:* Prothorax very short, dark brown; the postero-lateral areas membranous; a finger-like projection extends from near the lateral margin; a large circular pale spot on the mid-line based on the posterior margin but not attaining the anterior margin; postero-lateral corners pale; these three pale areas connected by a narrow pale posterior edge (fig. 2). Meso- and meta-thorax fuscous with extensive pale membranous areas at the leg bases and at the wing bases. Inner parapsidal furrows of mesonotum pale, narrowed anteriorly and mostly closed, a pale transverse stripe connects the two furrows, thus forming a pale, roughly H-shaped mark, a small tapering median stripe extends caudad a short distance from the transverse stripe; the outer parapsidal furrows pale, but somewhat obsolescent at and anterior to the wing base. *Legs:* Fore legs (fig. 7) shorter than middle or hind legs; tarsi two segmented; femora dark brown, ventral (posterior) edge pale; tibia and tarsus pale brown, darkest dorsally; claws (fig. 8) large and bulb-like, similar, pale brown. Middle and hind legs (figs. 5 and 6) light brown, darkest dorsally; femora darkest, with pale ventral and dorsal edges; tarsi three-segmented. *Wings:* Bright reflection of blue or purple may show in alcoholic specimens; reflections probably evident in living specimens. Venation as in figures 9 and 10; medium brown. Microchaetae cover the base of the fore wing, the costal border, all veins, and the posterior edge, while the membrane between the veins is covered with microtubercules. The entire surface of the hind wing is covered with microchaetae. *Abdomen:* Abdominal tergites uniformly dark brown; a dark narrow stripe near the pleural and posterior margins and on the anterior margin, a pair of submedian dark streaks or spots near the middle of each tergite; these better developed on the anterior tergites. Abdominal sternites one to eight considerably paler than tergites, the edges slightly darker; paired submedian markings consist of pale streaks or spots outlined in dark brown, on the anterior sternites these are largely streaks with one or two detached spots, on subsequent sternites the streak breaks up into spots; tergites slightly paler between these markings; sternite nine with the anterior part dark brown, the posterior part pale, margins dark, sternite ten dark with pale central area; penes as in figures 4 and 13; no genital forceps present. Cerci and terminal filament light brown with conspicuous setae at each joining (fig. 11).

Female imago.—Length: body 9–10; wing 7–8; tails 2–3 mm. *Head:* Similar to that of male; eyes considerably smaller, contiguous dorsally (fig. 3). Thorax similar to that of male. Legs twisted and obsolescent.

Abdominal tergites similar to those of one to eight of male, but paler. Sternites similar to those of one to eight of male, but with median line paler and limited by poorly defined spots and streaks. Tails brown, darker than those of male, without setae (fig. 12).

Nymph.—Spieth's (1937) description of *H. ammophila* adequately covers the characteristics of *H. dolani* except in a few details, which are as follows: *Length:* Mature female nymph—body 11.5 mm., caudal filaments 3.2 mm.; mature male nymph—body 9.5 mm., caudal filaments 2.2 mm. *Head:* Median carina present between the antennal bases. In ventral view, when the forelegs are pulled forward, the multibranched gills of the maxillae can be seen projecting posteriorly between the bases of the legs to form a dense clump of white, thread-like structures protected by the very thick, overlaying labium. Mouthparts (figs. 16–22) are so large that they project posteriorly to the bases of the mesothoracic legs, forming a large and conspicuous clump under the head. *Legs* (figs. 27–29): Tibia of prothoracic leg strongly bowed with the proximal portion curved so that it fits into a groove in the femur. The groove of the fore femur extends almost the entire length of the ventral surface, but is deepest in the distal half, just before the origin of the long fringing hairs on the proximal half of this leg segment. At the angle of the curve of the tibia, it arches down in such a way that the long hairs bordering its inner surface are brought directly below the mouthparts so that when the tibia is folded into the femoral groove, the hairs of the tibia and of the femur form a continuous band. Thus a mass of hairs is brought directly under the mouth. *Abdomen:* Coloration of abdominal segments rather variable,

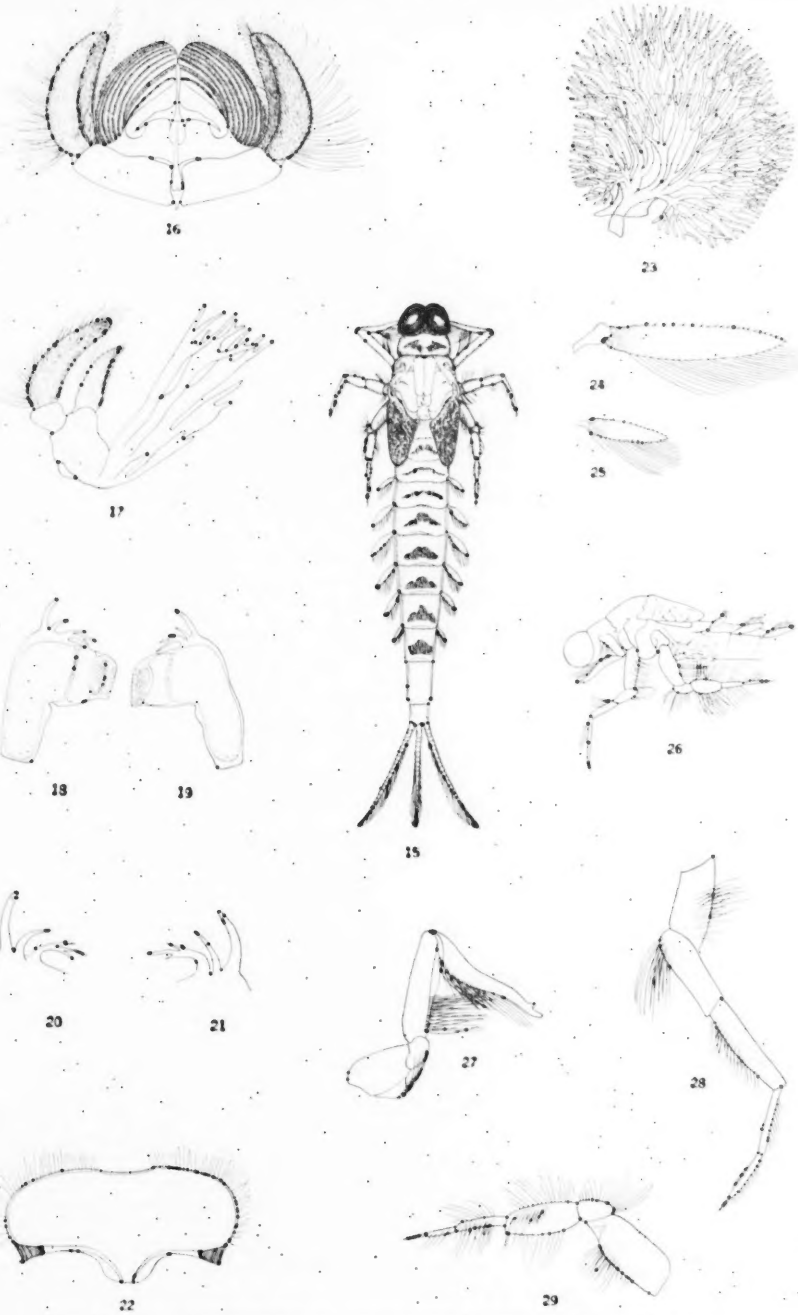


FIG. 15 to 29.—*Homoeoneuria* sp., nymph, from Homochitto River, Mississippi.

FIG. 15.—Male nymph, dorsal view.
FIG. 16.—Labium, ventral view.
FIG. 17.—Left maxilla with attached gill.
FIG. 18.—Left mandible.
FIG. 19.—Right mandible.
FIG. 20.—Lacinia mobilis and canines, left mandible.
FIG. 21.—Lacinia mobilis and canines, right mandible.
FIG. 22.—Labrum.
FIG. 23.—First gill.
FIG. 24.—Fourth gill.
FIG. 25.—Seventh gill.
FIG. 26.—Anterior portion of nymph, lateral view.
FIG. 27.—Prothoracic leg.
FIG. 28.—Mesothoracic leg.
FIG. 29.—Metathoracic leg.

some nymphs virtually lacking the brown bands on the tergites, while they are broken in others. Dorsally, there is a covering of short spines rather heavily distributed over the entire surface, exclusive of the portion of the tergites overlaid by the gills. The sternites, except for that of segment one, are covered by long hairs, sharp spines, or both. On sternites two, three, and four there are long, posteriorly-directed hairs; those on two and three so arranged that they form a U-shaped pattern with the opening of the U directed anteriorly. The hairs on sternite two are concentrated at the postero-lateral angles, while on sternite three they are present along the lateral and posterior margins. There are also a few small spines present on sternite three. Sternite four has hair-like spines on the posterior margin and the postero-lateral angles of the segment. (This pattern of hairs and hairlike spines concentrated near the first pair of gills may form a protective covering to keep silt and trash away from them.) Other sternites covered with short, coarse spines, and sublateral rows of long hairs. The rows of hairs become sparser posteriorly and are absent from segments nine and ten. Median portion of posterior border of sternite nine prolonged posteriorly; the prolongation excavated with the lateral corners of the excavation terminating in spines. Between the spines there is a row of short spinules. Gills two to seven margined (figs. 24 and 25) on outer edge with short spines; inner edge bordered with long hairs.

Holotype. GEORGIA: Savannah River, October 20, 1951, T. Dolan IV and S. S. Roback (UU).[5] *Allotype.* Same data. *Paratypes.* GEORGIA: Savannah River, July 9 (UF) and 22 (UF, UU) 1952, adults, collected by D. C. Scott; August 27, 1955, nymph (ANSP), September 2 (UF), June 28, 1951 (JRT, UU), October 20, 1951 (UU, ANSP), adults, collected by T. Dolan and S. S. Roback; November 2, 1951, nymphal exuviae, collected by T. Dolan IV and S. S. Roback (ANSP); Savannah River, Brigham's Landing, August 27, 1955, nymph, collected by S. S. Roback (ANSP). SOUTH CAROLINA: Greenville County, South Saluda River, July 28, 1953, nymph, collected by M. J. Westfall (UF); Savannah River, 8 miles above Allendale Bridge, August 21, 1955, nymph, collected by S. S. Roback (ANSP).

Homoeoneuria ammophila (Spieth)

The description and figures of the nymph of this species are given by Spieth (1938: 1). We have found no way to distinguish the nymphs of the two (or more) species that we have studied. Further study of reared or associated material will probably result in the discovery of distinguishing characteristics.

Records.—INDIANA: White River, Hazelton, June 16, 1936, nymphs, collected by H. T. Spieth (AMNH); White River, Decker, July 27, 1932, nymph, collected by S. Denham. ILLINOIS: Hillsdale, Rock River at mouth of Canoe Creek, July 30, 1925, nymph, collected by R. E. Richardson (INHS); Rock River at foot of Lephardt's Island, July 30, 1925, nymph, collected by R. E. Richardson (INHS).

We are tentatively considering the males described below as representing the adult of *H. ammophila*.

Male imago.—The description of *H. dolani* will apply equally to the males which we tentatively assign to this species, except as follows. *Length:* body 10; wing 9–10 mm.; terminal filament and cerci, 10 mm. Spot on mid-line of prothorax quadrate (rather than circular). Abdominal tergites dark brown, a dark thin stripe near the pleural margin; posterior margin marked with a narrow fuscous stripe on tergites one and two, this stripe becoming progressively better developed in the middle area of segment to tergite seven, tergites eight and nine wholly fuscous. Penes as in figure 14. Cerci and terminal filament white with conspicuous setae at each joining.

If adults of *Homoeoneuria ammophila* can be reared or collected from the White River at Hazelton, Indiana, or the nymphs secured of the Kansas males, the latter might prove to be a separate species, although it is more likely that these males are *Homoeoneuria ammophila* (Spieth).

Records.—KANSAS: Wyandotte Co., Kansas River, ¼ m. SE Bonner Springs, two males, W. L. Peters (in Peters' personal collection).

Homoeoneuria sp.

These nymphs, which are unassociated with adults, we are unable to assign to any particular species, but include the records here.

Records.—FLORIDA: Escambia County, Escambia River at Florida Highway 4, August 12, October 23, 1954, nymphs, collected by C. D. Hynes and Lewis Berner (UF). MISSISSIPPI: Franklin County, Homochitto River at U. S. Highway 98, June 5, 1956, nymphs, collected by C. D. Hynes and Lewis Berner (UF, UU). NEBRASKA: Kearney, September 5, 1951, nymphal exuviae, collected by G. F. Edmunds (UU). TEXAS: Guadalupe River, S. of Victoria, September 4, 1950, nymphal exuvia, collected by T. Dolan IV (ANSP).

BIOLOGY OF *Homoeoneuria*

A series of nymphs of *Homoeoneuria* sp. collected at the Homochitto River (fig. 1) in Mississippi on June 5, permitted limited observations of the habitat and habits of the insects. At the time collections were made, the river

[5]The collections where specimens are located are indicated by abbreviations as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CNC, Canadian National Collections; INHS, Illinois State Natural History Survey; JRT, collection of Jay R. Traver; ROM, Royal Ontario Museum, Toronto; UF, University of Florida; UM, University of Massachusetts; UU, University of Utah.

level was low, so low in fact that the water occupied only half the River basin. At few places was the depth of the stream more than 3 feet, a reflection of the semi-drought conditions which were prevalent in the southeast during 1956. Nevertheless, the water flowed rapidly so that considerable effort was needed to wade upstream. The stream bottom was clean-swept, composed mostly of loose, shifting sand with pebbly stretches, and there was no attached vegetation.

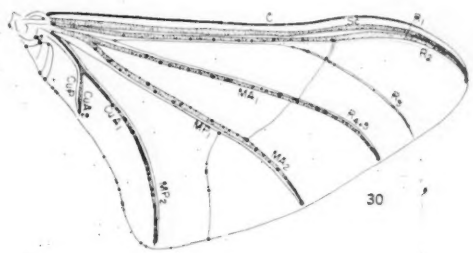
By stirring the sand by foot and holding a screen downstream as many as six to eight nymphs could be collected at each attempt. The living nymphs are very transparent so that they were at first difficult to see against the collecting screen; however, with a little practice, the insects could be picked up with ease. Against a white background, the bodies of some of the nymphs had a distinct greenish tinge and many showed brownish annulations on the abdomen. A few of the nymphs had blackened wing pads indicating that they were virtually ready to emerge.

To determine exactly where the nymphs were living, one person stirred the very top level of the sand bottom, perhaps the upper inch, and a second held a screen downstream. Only a single nymph was taken. By stirring somewhat deeper in the same area many additional specimens were taken. Further observations indicated that the nymphs live one to two inches below the surface of the sand.

Nymphs placed in a pan of water with no sand proved to be extremely awkward swimmers. In the water, the body was vibrated vigorously dorso-ventrally, but the insect scarcely moved. After a few seconds in this attempt to swim, the nymph turned over onto its dorsal surface, sank to the bottom of the pan and rested. When sand from the stream bottom was placed in the pan and the insects came in contact with it there was an immediate reaction. The body vibrated rapidly in the same pattern demonstrated in the weak swimming attempt, and this resulted in the very rapid disappearance of the nymphs into the sand. Apparently, this vibrating not only stirs up the sand so that it is pushed away from the nymph, but also permits rapid covering of the body. Orientation of the nymphs in the sand is probably upstream as evidenced by the apparent feeding mechanism. The forelegs, with their long hairs, are held directly below the mouthparts which are also covered with long hairs. Food is filtered from the loose sand, and the animal grazes on the material caught on the hairs. An examination of contents of the digestive tract showed only that the food was so thoroughly macerated that it could not be identified. The green color of some of the living nymphs may indicate that algae make up some of the food of this species.

Specimens collected from the Escambia River, Florida, were taken under similar circumstances to those taken from the Homochitto. The Escambia was at the lowest level observed in years and it was, therefore, possible to work in the stream bed with a screen. A few nymphs were taken by stirring the shifting sand bottom and collecting them downstream on the screen.

The period of emergence extends from at least early June through late October. Adults have been taken as late as October 20 from the Savannah River. On the basis of collections made thus far, the nymphs of *Homoeoneuria* appear to be inhabitants of larger streams.



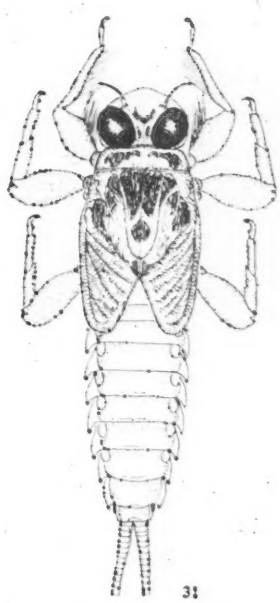


FIG. 30.—*Lachlania powelli*, wing of male imago.
FIG. 31.—*Lachlania powelli*, dorsal view of male nymph.

Genus **Lachlania** Hagen

The genus *Lachlania* was erected by Hagen (1868) for the species *Lachlania abnormis* Hagen from Cuba. Needham and Murphy (1924) referred a nymph from Guatemala to the genus. The first record of the genus north of Mexico was established by Ide (1941: 154) who described *Lachlania saskatchewanensis* from Saskatchewan.

The genus was next discovered in Utah by Edmunds (1948, 1951), who obtained a species which was named *Lachlania powelli*. The species was reared, thus positively associating the nymphs and adults, confirming the association previously established by Needham and Murphy. A few specimens of *L. powelli* have subsequently been collected from the type locality, but the known range of neither species of *Lachlania* has been extended.

The genus *Lachlania* (s.l.) is a very distinct one of widespread occurrence in the Americas. It is probably most closely related to the genus *Spaniophlebia* which it resembles in both the adult and nymphal stages, but any statement concerning the relationship of the New World Oligoneuriidae seems premature until we have a better knowledge of the genera *Oligoneuria* and *Oligoneuriodes*. There seems to be little reason for retaining subgeneric groupings in *Lachlania* in the present state of our knowledge.

Lachlania saskatchewanensis Ide

This species was described from a single female; the species differs from the only other known from North America north of Mexico, *L. powelli* Edmunds, as cited under that species. It is probable that the discovery of this specimen on the surface of a salt lake was accidental.

Records.—SASKATCHEWAN: Stoney Lake, near Humboldt, September 5, 1940, collected by J. E. Moore and J. S. Thompson (ROM).

Lachlania powelli Edmunds

This species appears to be very similar to *L. saskatchewanensis* and may eventually prove to be synonymous, although the series of approximately fifty females of *L. powelli* from Utah differ consistently from the drawings and description of the single female of *L. saskatchewanensis* Ide. The former has a pair of large paramedian pale spots on the anterior margin, while the latter has a continuous pale band; *Lachlania powelli* has less curvature in the veins of the forewing and a relatively broader hind wing. Several other species of mayflies occupying similar habitats are common to the Green River of Utah and the Saskatchewan River area. *L. powelli* will rest as an established species only after a series of females, males, and nymphs of *L. saskatchewanensis* becomes available.

The nymphs of *Lachlania powelli* were found chiefly attached to sticks, other trash, and on the surface of rocks in rapids. The river in this area is essentially a "warm water" river, being occupied by such widespread introduced fish species as carp and channel catfish, and also by such native forms as the Colorado River squawfish, some forms of Gila, and by flannelmouth and humpbacked suckers. From the distributional data, it seems that other species of the genus occupy similar habitats.

The nuptial flight of *L. powelli* takes place in midmorning, and is characterized by very rapid flight which is probably similar to that of all the Oligoneuriinae. The subimaginal skin is shed while the insects are in flight, but the pellicle is not shed from the wings. This habit is probably found in all Oligoneuriinae. Additional observations on the biology of *L. powelli* have been published by Edmunds (1951).

Records.—UTAH: Green River at Hideout Canyon, 5800 feet elevation, Daggett County, nymphs and adults, August 9, 1947, September 3–4, 1947, September 5, 1948, September 11, 1950, September 9, 1952, September 18, 1954 (UU, UF, AMNH, JRT, UM, CNC, CAS), all collected by G. F. Edmunds.

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OBSERVATIONS ON THE SURVIVAL OF MOSQUITO PUPAE ON MOIST SOIL[1]

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ABSTRACT

Field observations were conducted on *Aedes nigromaculis*, *A. melanimon*, *Culex tarsalis*, and *C. stigmatosoma* on moist, heavy soils in Fresno and Yolo Counties, California. Pupae here were subjected to high temperatures, low humidities, and lack of free water. Even under these severe conditions large numbers of pupae remained alive 24 to 48 hours, and absence of standing water did not prevent emergence of adult mosquitoes. A simulated habitat designed to protect pupae from these elements appreciably enhanced survival and subsequent emergence. The findings indicate that larvicide operations, in order to assure a high degree of effectiveness, should take into account all damp depressions which may hold water periodically for relatively short periods of time.

While engaged in ecological studies on mosquitoes in irrigated cotton fields in West Fresno County, California, observations of *Aedes* pupae in transient puddles drew to our attention the phenomenon of drought resistance. Since this matter appeared to carry some significance in mosquito control operations, an effort was made to record pertinent observations systematically. Similar observations were made later in the Davis area of the Sacramento Valley.

While considerable attention has been given to the drought resistance of eggs of various species of *Aedes*, relatively little has been published concerning the resistance of mosquito pupae to drought.

Smith (Headlee, 1945) found that larvae of *Aedes sollicitans* (Walker) would survive a few hours in soft mud, and that pupae under similar conditions would survive as long as 24 hours and develop into adults. Nielsen and Nielsen (1953) made similar observations on *Aedes taeniorhynchus* (Wiedemann).

Bick and Penn (1947), working in the laboratory, found that pupae of *Aedes texans* (Meigen) were more resistant to drought than the larvae. Of major significance was the fact that lack of free water did not prevent emergence. Imagines emerged from 94 percent of the pupae under drought conditions. The maximum time under continuous drought was 120 and 96 hours, respectively, for third and fourth instar larvae. Bick (1948) obtained 292 adults (*Culex quinquefasciatus* Say) from 298 pupae maintained under continuous drought.

In California, Thurman and Mortenson (1950) observed that pupae of *Aedes nigromaculis* (Ludlow) were able to resist drying to a considerable degree in irrigated pastures. Emergence of adult mosquitoes was observed at least 29 hours after visible water had disappeared from a "pot-hole". Husbands (1952) found that as a pasture aged, and as ponding areas increased, the shallow extension of standing water into adjacent areas produced conditions favorable for the survival of pupae that were stranded on damp soil as the water receded. Stranding of pupae resulted in the successful emergence of large numbers of adults from such areas. Estimates by Husbands of the number of adults produced in pastures by this method show that as high as 50 percent of *A. nigromaculis* adults can originate from stranded pupae. Thus, mosquito control operations should take into rather careful account all areas where water will remain long enough to produce late fourth instar larvae or pupae.

METHODS

A number of mosquito sources were located in the field which served as a supply of mosquito pupae. Daily inspections allowed us to follow closely the growth and development of the larvae. When the larvae had reached the fourth instar, inspections were made twice a day (morning and afternoon) in order to observe as closely as possible the development and duration of the pupal stage.

Large numbers of pupae were collected in quart jars containing water from the pool and transported to the study sites. If the soil did not contain sufficient moisture from irrigation, water was added from a nearby irrigation canal and time was allowed for penetration.

The study site in Fresno County was a cotton field characterized by heavy Temple clay soil. The site in Yolo County was adjacent to a rice field. The specific soil type was not determined; however, in the area, the impervious subsoil is essentially clay and adobe clay and is well suited to rice culture.

After the soil had been prepared, the area to be occupied by a cage was outlined. Pupae were transferred into white, shallow, enamel pans to facilitate removal and counting. After the allotted number of pupae had been placed on the moist soil, a screened cage was put in place. A recorded number of remaining pupae were placed in jars of water and brought to the laboratory. Screened floats ($\frac{1}{4}$ inch mesh hardware cloth) were available to the newly emerged adults.

Two types of cages were used in these experi-

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ments. One type was 14 inches square and 8 inches in height. The cage was covered on all sides except the bottom with 16 mesh wire screen. The bottom of the cage was open and supported by a two inch metal strip which was pressed into the moist soil to prevent overturning. There was provision at the bottom of the cage for the insertion of a metal slide. Two cages of this type were used. They were designated as Cage A and Cage B.

The second type of cage was 16 inches long, 9 inches wide, and 16 inches in height. Except for dimensions, these cages were similar to those described above. The same area, 144 square inches of soil surface, was available to pupae in both types of cages. Cages of the second type were designated as Cage C, D, and E in the experiments.

jars containing water from the main irrigation canal and transported to the laboratory in Fresno. A daily record was kept of the adult emergence from these pupae.

Almost all field tests were based on a 24-hour exposure period. However, a few were extended to 48 hours. At the end of the exposure period each cage was examined for emergence. Adult mosquitoes were coaxed into the upper portion of the cage before the slide was put into place. Plastic strips were placed against the two sides of the cage to block off any remaining specimens, and as the cage was slowly tilted backwards these were collected with an aspirator. After the adults had thus been collected, the area occupied by the cage was quickly covered with a piece of cheesecloth as the entire cage was lifted out of position. An additional collection was then made

FIG. 1.—Unprotected pupae on moist soil.

Pupae were designated as "protected" or "unprotected" according to whether or not they were covered by a layer of wet straw. The straw, when used, was bridged across two sticks so that there was approximately ¼ inch of space between the pupae and the matting.

Thermometers were inserted in the soil to a depth of ½ inch in both types of cages. Air temperature and relative humidity readings were taken periodically. Samples of soil were tested to determine moisture content at the start and end of each test.

Samples of surviving pupae were placed in

of adults remaining on the ground by carefully rolling back the cloth. On occasions, adults were observed to be hiding in small cracks in the soil. A record was kept of the few adults which escaped. The cage was covered with a large cardboard box and the adult mosquitoes were chloroformed immediately and placed in pill boxes. A careful examination was then made of all pupae left on the soil. Partially emerged adults were recorded and placed in separate pill boxes.

The next step was that of collecting the surviving pupae. It was not difficult to detect live

FIG. 2.—Protected pupae on moist soil.

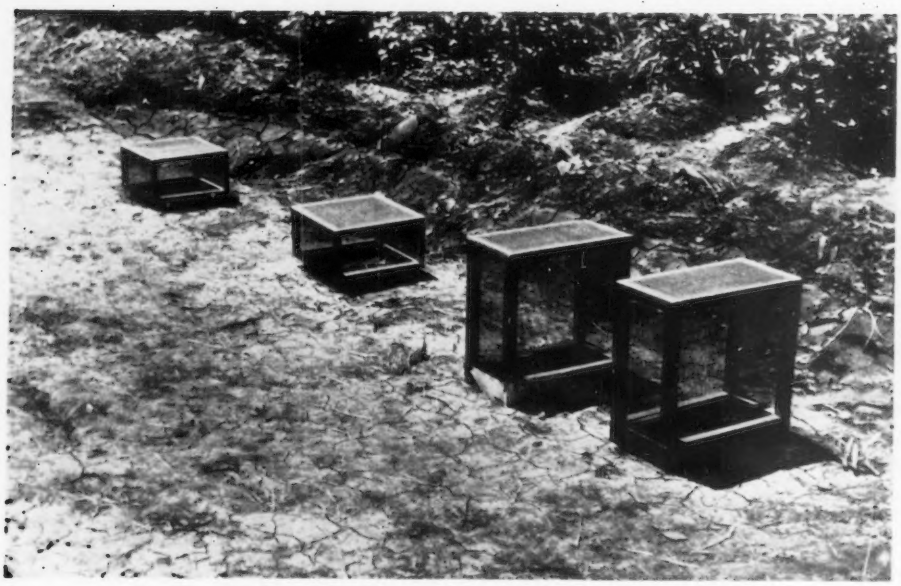

FIG. 3.—Cages in the field containing protected and unprotected pupae.

pupae on the soil, even after an exposure period of 24 or 48 hours. By means of moistened forceps or a small moistened twig, pupae were transferred to jars of water. When touched with these wet instruments, the surviving pupae were quick to respond to the presence of moisture. Pupae were placed in two separate jars, one for protected pupae and the other for unprotected pupae. These were transported to the laboratory and a record was kept of emergence.

The sources of supply for the pupae used in the Fresno tests were irrigated pastures and a cotton field drainage area. In Sacramento tests, pupae were collected from rice field seepage areas.

The approximate age of pupae used in these tests was as follows:

8– 9 hours—Experiment 22
12–18 hours—Experiment 20
24 hours—Experiments 9–11–14–16–17–18–24
48 hours—Experiments 8–10–12–13–15–19–21–23
Undetermined—AE–1 to AE–6, inclusive

The species of mosquitoes studied included *Aedes nigromaculis* (Ludlow), *Aedes melanimon* Dyar, *Culex tarsalis* Coquillett, and *Culex stigmatosoma* Dyar.

TABLE I

A Comparison of Emergence in the Field of Unprotected and Protected Pupae

	Estimated Age of Pupae	Field Tests	Pupae Used	Adults Emerging in the Field	Surviving Pupae	Adults From Surviving Pupae
Unprotected	8–9–12–18–24 hrs.	8	2865	243 (8.4)%	1018 (35.5)%	382 (37.5)%
Unprotected	48 hrs.	6	2400	1334 (55.0)%	133 (5.5)%	26 (19.5)%
Protected	8–9–12–18–24 hrs.	8	4063	723 (17.7)%	2179 (53.6)%	954 (43.7)%
Protected	48 hrs.	6	3100	1850 (59.6)%	426 (13.7)%	182 (42.7)%

TABLE II

Incomplete Emergence of Unprotected Pupae

Test Number	Percent Incompletely Emerged	Test Number	Percent Incompletely Emerged	Test Number	Percent Incompletely Emerged
9	2.0	17	4.0	23	4.0
10	10.5	18	8.5	AE–1	15.5
12	4.3	19	11.7	AE–2	12.0
14	1.7	20	3.7	AE–3	27.0
15	9.5	21	12.0	AE–4	12.0
16	2.0	22	1.0	AE–5	12.0
				AE–6	23.3

TABLE III

Incomplete Emergence of Protected Pupae

Test Number	Percent Incompletely Emerged	Test Number	Percent Incompletely Emerged	Test Number	Percent Incompletely Emerged
13	3.3	19	4.1	AE–2	24.0
14	1.0	20	4.0	AE–3	27.0
15	14.0	21	7.8	AE–4	14.0
16	0.6	22	0.8	AE–5	8.0
17	4.5	23	2.0	AE–6	13.3
18	5.8	24	19.0		

TABLE IV

SUMMARY OF DATA ON PROTECTED PUPAE IN CAGES B, D, AND E

Field Test Number	Total Number of Pupae Used	After 24 Hours			Emergence of Remaining Live Pupae in Laboratory
		Emerged	Remaining Pupae		
			Alive	Dead	
11	63	6[c]	0	57	0
13	1,000	577[a]	260	163	124[a]
14	600	73[a]	350	177	155[b]
15	600	301[b]	12	287	4[b]
16	600	55[a]	415	130	139[b]
17	600	11[c]	322	267	38[b]
18	600	163[a]	334	103	158[d]
19	600	421[a]	65	114	27[e]
20	600	270[a]	206	124	92[f]
21	600	339[d]	69	192	16
22	600	48[a]	516	36	363[a]
23	200	144[a]	20	36	11[b]
24	400	97[b]	36	267	9[b]
AE-1	45	3	5	37	5[c]
AE-2	25	2[c]	16	7	13[c]
AE-3	100	12[c]	36	52	26[c]
AE-4	100	1[c]	67	32	42[c]
AE-5	100	3[c]	80	17	68[c]
AE-6	150	38[a]	72	40	67[c]

[a] 100% *A. nigromaculis*
[b] 100% *A. melanimon*
[c] 100% *C. tarsalis*
[d] 92% *A. nigromaculis*
8% *A. melanimon*
[e] 4% *A. nigromaculis*
96% *A. melanimon*
[f] 62% *A. nigromaculis*
38% *A. melanimon*
[g] 44% *A. nigromaculis*
56% *A. melanimon*
[h] 100% *C. stigmatosoma*

TABLE V

SUMMARY OF DATA ON UNPROTECTED CAGES A AND C

Field Test Number	Total Number of Pupae Used	After 24 Hours			Emergence of Remaining Live Pupae in Laboratory
		Emerged	Remaining Pupae		
			Alive	Dead	
9	400	25[a]	138	237	83[a]
10	400	265[a]	1	134	1[a]
11	65	2[b]	0	63	
12	600	466[c]	24	110	14
14	400	39[c]	92	269	10
15	400	84	1	315	0
16	400	36	91	273	0
17	400	0	27	373	0
18	400	13	148	239	19[c]
19	400	197[a]	41	162	0
20	400	124[a]	169	107	80[d]
21	400	198[c]	57	145	11[c]
22	400	4[a]	353	43	190[c]
23	200	124[a]	9	67	0
AE-1	45	3[b]	13	29	3[b]
AE-2	25	2[b]	18	5	9[b]
AE-3	100	3[b]	26	71	5[b]
AE-4	100	0	44	56	5[b]
AE-5	100	1[b]	47	52	12[b]
AE-6	150	12[b]	68	70	9[b]

[a] 100% *A. melanimon*
[b] 100% *C. tarsalis*
[c] 100% *A. nigromaculis*
[d] 75% *A. nigromaculis*
25% *A. melanimon*
[e] 66% *A. nigromaculis*
34% *A. melanimon*
[f] 57% *A. nigromaculis*
43% *A. melanimon*

OBSERVATIONS

Meteorological Observations—Maximum daily temperatures in the summer are reached between 4:00 and 5:00 p.m. (Pacific Daylight Saving Time) in the San Joaquin and Sacramento Valleys (Fresno and Yolo Counties, respectively).

During July 1955, (field tests 8–15) air temperatures ranged from 74°–101° F., the relative humidity from 25–47 percent, the temperature of the moist soil (protected) from 70°–94° F., and the temperature of the dry soil adjacent to the cages from 94°–134° F.

In August 1955, (field tests 16–22) air temperatures ranged from 79°–96° F., the relative humidity from 34–60 percent, the temperature of the moist soil (protected) from 78°–96° F., and the temperature of the dry soil from 90°–130° F.

During September, (field tests 22–24) the air temperature ranged from 68°–96° F., the relative humidity from 32–58 percent, the temperature of the moist soil (protected) from 68°–90° F., and the dry soil from 96°–123° F.

During September in Yolo County (field tests AE–1–6) the air temperature ranged from 66°–98° F., the relative humidity from 20–89 percent, the temperature of the moist soil (protected) from 52°–94° F., and the dry soil from 64°–126° F. High and low air temperature readings within the cages ranged from 50°–112° F.

Soil Moisture.—The moisture content of the wet soil samples at the start of the test ranged from 13.9 to 38.9 percent during the month of July. Moisture loss in the unprotected soil samples ranged from 1.8 to 12.5 percent, and in one protected soil sample the loss was 9.9 percent.

During August, moisture loss in unprotected soil ranged from 1.8 to 13.8 percent, and in one protected soil from 1.6 to 10.1 percent. In exposed soil (between the cages) the loss ranged from 6.1 to 6.7 percent. The moisture content of wet soil at the start of the tests ranged from 17.7 to 23.1 percent.

During September, the moisture loss in 24 hours for unprotected soil ranged from 11.1 to 12.8 percent, and in protected soil from 6.9 to 9.0 percent. Between the cages, the exposed soil showed a loss of 6.1 to 6.7 percent. The percent moisture content of the wet soil at the start of the test ranged from 22.1 to 23.1 percent.

During the 48 hour exposure period the loss of moisture of the unprotected soil was 15.5 percent and for the protected soil 13.6 percent. The loss was 18.0 percent for the exposed soil between the cages. The moisture content of the soil at the beginning of the test was 19.1 percent.

In Yolo County the moisture content of the wet soil at the start ranged from 19.0 to 24.3 percent. The loss in the unprotected soil ranged from 4.3 to 10.9 percent, and from 5.3 to 11.0 percent in the protected soil.

Emergence in the Field.—In Table I a comparison is made of results obtained with unprotected and protected pupae. Tables IV and V summarize adult emergence in the field from unprotected and protected pupae, respectively.

Of major significance is the fact that lack of

TABLE VI

SUMMARY OF DATA ON CONTROL PUPAE IN THE LABORATORY (IN WATER)

Field Test Number	Total Number of Pupae Used	Number of Adults Emerged								Percent Emergence Adults	
		24 Hours				48 Hours					
		Total	Species			Total	Species			24	48
			A. nigromaculis	*A. melanimon*	*C. tarsalis*		*A. nigromaculis*	*A. melanimon*	*C. tarsalis*		
14	400	151	62	89	—	338	64	274	—	38	84
15	400	381	5	376	—	382	5	377	—	95	96
16	400	131	47	84	—	316	47	271	—	33	80
17	400	62	—	—	61[a], 6	352	—	—	285[a], 67	17	88
18	400	234	234	—	—	373	342	31	—	58	93
19	400	327	285	42	—	357	286	71	—	82	89
20	600	417	394	23	—	499	405	94	—	70	83
21	600	491	454	37	—	506	454	52	—	82	84
22	550	218	218	—	—	479	475	4	—	40	87
23	600	456	446	10	—	498	449	49	—	76	83
24	800	363	—	—	—	670	—	670	—	45	84
AE-1	40	16	—	—	16	37	—	—	37	40	92
AE-2	25	10	—	—	10	25	—	—	25	40	100
AE-3	100	48	—	—	48	95	—	—	95	48	95
AE-4	100	43	—	—	43	93	—	—	93	43	93
AE-5	100	70	—	—	70	99	—	—	99	70	99
AE-6	200	177	—	—	177	193	—	—	193	88	96

[a] *C. stigmatosoma*

free water did not inhibit emergence, even under severe field conditions. Surprisingly large numbers of pupae also remained alive for a period of 24 to 48 hours under these conditions. Adults which emerged in the field were observed to be strong and very active.

Of the mosquitoes which emerged from protected pupae, 46.1 percent were males and 53.9 percent were females. In the case of unprotected pupae 37.0 percent were males and 63.0 percent were females.

A record was kept of adults found in various degrees of incomplete emergence. If the tarsal segments were attached to the pupal exuviae, the imago was considered incompletely emerged. The results are recorded in Tables II and III. The total number of incompletely emerged adults in the field was 842, of which 397 were from unprotected pupae, and 445 from protected pupae.

Emergence in the Laboratory.—Table VI summarizes the control data on pupae which emerged in the laboratory. In the Fresno tests emergence in the laboratory ranged from 79.5 to 95.5 percent. In the Yolo County tests, adult emergence in the laboratory ranged from 92.5 to 100 percent. The smaller number of pupae and the shorter distance of transportation in the latter tests may account for the higher emergence of adults.

Control pupae were used for several reasons: (1) to determine the adult emergence in water, (2) to supplement identification of adults in case of failure in the field, and (3) to corroborate visual observations on estimation of the age of the pupae.

Of the adults that emerged in the laboratory during the first 24 hour period, 51.6 percent were males and 48.4 percent were females. During the second 24 hour period 39.2 percent were males and 60.8 percent were females.

Of the adults which emerged in the laboratory from protected pupae, 35.3 percent were males and 64.7 percent were females; from unprotected pupae 42.6 percent were males and 57.4 percent were females.

It may be significant that many adults emerging in the laboratory from unprotected pupae were weak and inactive, whereas adults from protected pupae were stronger and more active. However, the adults emerging from control pupae in the laboratory were even more robust.

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The third volume of this series devoted exclusively to papers on the cerambycidae includes four revisionary studies; viz. African Prioninae by E. F. Gilmoure, and each of the tribes Petrognathini, Aemocerini and Astathini by S. Breuning. Twenty-three other papers of varying length are included. Practically all include useful keys and many of the cerambycid forms are nicely figured. None of the treatises go beyond the level of alpha taxonomy. The list of new names extends over 11 pages, single column, and represents *nomen nova* as well as *forma nova*. Many of the new forms are based upon unique holotypes and 162 are varietal. Very little to no information is given on host plants, general ecology, and seasonal occurrence. Presumably this situation reflects the character of the study material.

In a morphological sense these papers bring together a large amount of information useful in the identification of Cerambycidae principally for Africa and South Asia. But the writer, for one, does not relish the dose of varietal names based upon desultory, poorly annotated study material.

GEORGE B. VOGT.

TAXONOMIC AND BIOLOGICAL OBSERVATIONS ON THE GENUS HORNIA (COLEOPTERA: MELOIDAE)[1]

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ABSTRACT

Limited biological observations on several species of *Hornia* are reported from California, New Mexico, and the State of Chiapas in southern Mexico. Restudy of available adults and larvae of *H. minutipennis* Riley indicates that the subspecific name *H. m. occidentalis* should be applied only to populations from central and coastal California. The relationship of *H. mexicana* Dugès, from central Mexico, to *H. neomexicana* (Cockerell), from the southwestern United States, is not definitely known due to lack of specimens and to incomplete and inconsistent descriptions of the former. A previously unknown population from Chiapas is variable in the characters used to separate these species, and therefore *H. neomexicana* is considered to be a subspecies of *H. mexicana*. The Chiapas population is described as *H. mexicana blomi*, since its pattern of variation is distinctive.

Our knowledge of this genus has increased appreciably since the taxonomic revision of Linsley (1942) and the biological studies of Linsley and MacSwain (1942). Observations on the habits of *Hornia minutipennis* Riley in Alberta have been recorded by Hocking (1949) and in Wyoming, Idaho and Utah by Bohart and Selander (1955). Other data on several species of *Hornia* and their hosts have been accumulated from California, New Mexico and the State of Chiapas in southern Mexico. These are the subject of the following discussions.

Hornia minutipennis Riley

Hornia minutipennis occurs from California to New York and also is known from southern Canada. Populations from different parts of this wide range exhibit variations in the adult and larva morphology and in habits which may indicate subspecific segregates. Two subspecies, *H. m. minutipennis* and *H. m. occidentalis* Linsley, were recognized by Linsley (1942). Additional information, which has resulted from the studies of Hocking (1949) and Bohart and Selander (1955), raises questions concerning the present definition of these subspecies. Although the situation cannot be clarified at this time, a review of our present knowledge is of value.

The adult male of *H. minutipennis* was described by Riley (1877) as having sclerotized bands on all of the abdominal terga and the tarsal claws simple, without an inner basal spine. A similar condition of the tarsal claws was described for the female. The adult male of *H. m. occidentalis* was found by Linsley (1942) to have the first two sclerotized bands of the abdomen feebly developed or absent and the tarsal claws with a distinct inner basal spine. The female also has a tarsal spine. Subsequently, Selander (Bohart and Selander, 1955) examined the "holotype" of *H. minutipennis* Riley and found that each tarsal claw had a basal spine. Selander also determined that the degree of sclerotization of the first and second abdominal tergites of a number of males was quite variable and is of no particular diagnostic value in separating races of *H. minutipennis*. Comments regarding adults of *H. minutipennis* which were received from the late H. S. Barber in December of 1949 are also of interest. "I am much puzzled as to the supposed "Type" of *Hornia minutipennis* Riley. This species was discovered in cells of *Anthophora* at Carondelet, Mo. (6 miles south of St. Louis) on Oct. 9, 1877 by Theo. Pergande, whose note on this find I have just reread. Only 3 adults were in his material at that date and he sent them (or some of them) to George Horn. Subsequent notes, which he must have written, are not now available, probably having been taken over by his friend and leader, C. V. Riley, who less than a month later (Nov. 5, 1877) read his paper on *Hornia* stating that he had found the species "on four different occasions" and that he had examined 4 males and 1 female. Pergande and Riley must have been keenly active in that short period but Riley did not mark his type specimens. Two greatly shrunken pinned specimens, ♂ ♀, in our collection were probably mounted by Pergande later and labeled with his note number to serve as reference samples in the pinned collection and, of these, the male was labeled as type by Linell after Riley's death, and was catalogued as type by Schwarz after Linell died, but both of these acts ignored Riley's alcoholic collection from which I now find a vial, containing 4 male and 5 female adults, which I believe was the lot from which Riley picked out the four better looking males and one female, which are mentioned in his hastily prepared description. The best one of these males shows that it was impaled from behind as if to hold it under a lens for more careful examination, and I believe it was this specimen which

[1]The observations on the habits of species occurring in Mexico are part of a series of studies made possible by grants-in-aid from the Associates in Tropical Biogeography, University of California. Accepted for publication December 16, 1957.

Riley used in making the dorsal and lateral drawings published with his original description. Before perceiving this latter possibility I had prepared this male and three of the associated females to be sent to you as a loan and now suggest that if you accept the above hypothesis, and are publishing on *Hornia*, it might be well to designate it as Lectotype selected from the originally mentioned 5 Cotypes."

"A few years later Hubbard, being with Schwarz and Pergande in this city, became interested in *Hornia*, looked for it in the clay banks where streets had been cut through near where our office building now stands, and easily found it, securing eggs and triungulinids. Shortly thereafter Koebele, who also worked with Schwarz and Pergande, easily found what was then misidentified as *minutipennis* at Alameda and, prompted by Schwarz's story and Hubbard's samples, I hunted for and found it about 1905. This latter colony on the river bank some 5 miles northeast of Hubbard's find, was often used to entertain visitors, Champion 1915 (Ent. Mo. Mag., vol. 51, p. 123) noting the live specimens his son and I had dug out in late November 1914. I became very curious about the differences in tarsal claws shown by specimens from here, and from Alameda but felt we needed many more locality samples."

Barber's comment concerning the Alameda, California, specimens was prompted by the well-developed tarsal spines of these specimens which are similar to those from other localities in California. By contrast, Hocking's specimens from Alberta have the minute spines more commonly found in eastern specimens while those of Bohart and Selander are similar in development to those from California. Thus, on the basis of these adult characters alone, no racial segregates appear to be recognizable although there are qualitative differences between most populations.

The characteristics of the first instar larvae are less well known than those of the adults. As mentioned previously (MacSwain, 1956), a clarification of the subspecies of this widely distributed and variable species cannot be accomplished until larvae of the nominate subspecies from the type locality are available. The only specimens available from the eastern United States are those of Pergande from Washington, D. C., referred to above. Morphologically they may be characterized as follows: mandibles bearing eight teeth; third antennal segment slightly longer than second segment; maxillary palpi with third segment about one and one-half times as long as second. Specimens from Alberta are similar in the development of the mandibles and maxillary palpi but the third antennal segment is subequal to or shorter than the second segment. Larvae collected from 16 miles north of Mt. Pleasant, Utah, previously reported by Bohart and Selander (1955), are like those from Alberta but possess nine or ten teeth in each mandible. Larvae, from a previously unreported population in the White Mountains of eastern California (see below), are dark brown, have seven (rarely eight) mandibular teeth, the third segment of the maxillary palpus is distinctly longer than the second and the last two antennal segments are about subequal. Therefore, each of these four populations can be distinguished from the others. However, larvae from four widely separated populations in western California, which have been described by MacSwain (1956), are similar to each other and also may

TABLE I

SIZE OF EXPANDED FIRST INSTAR LARVAE OF *Hornia*

SPECIES	LOCALITY	SIZE OF SAMPLE	LENGTH IN MM.		
			Minimum	Maximum	Average
minutipennis minutipennis	Washington, D. C.	10	1 6	1 75	1 70
minutipennis minutipennis	Edmonton, Alberta	5	1 5	1 55	1 54
minutipennis minutipennis	Mt. Pleasant, Utah	15	1 45	1 6	1 53
minutipennis minutipennis	White Mts. California	20	1 5	1 75	1 64
minutipennis occidentalis	Montara, California	8	1 8	1 9	1 85
minutipennis occidentalis	Bakersfield, California	10	1 65	1 8	1 75
minutipennis occidentalis	Marsh Creek, California	11	1 8	1 9	1 83
minutipennis occidentalis	Pinnacles, California	7	1 55	1 8	1 72
boharti	Pinnacles, California	10	1 6	1 85	1 75
boharti	Bakersfield, California	31	1 8	2 0	1 89
boharti	Little Lake, California	24	1 65	1 9	1 80
mexicana neomexicana	Loving, New Mexico	13	1 75	1 85	1 79
mexicana blomi	San Cristobal las Casas, Chiapas	29	1 8	2 1	1 99

be separated from the other four populations by the following combination of characters: mandibles bearing six or seven teeth; second and third segments of maxillary palpus subequal and third antennal segment distinctly shorter than second segment. Also, the larvae from these populations are larger than those from other areas (Table I).

The hosts of *H. minutipennis* are of interest. The most widely distributed of these is *Anthophora bomboides* Kirby which is presently subdivided into seven subspecies in America north of Mexico (Michener, 1951). *H. minutipennis* has been collected in association with the various subspecies as follows: *A. bomboides bomboides* Kirby from New York (Linsley, 1942); *A. b. sodalis* Cresson from Alberta (Hocking, 1949); *A. b. neomexicana* Cockerell from Idaho and Utah (Bohart and Selander, 1955), California (new record)[2] and *A. b. stanfordiana* Cockerell from California (Linsley, 1942, MacSwain, 1956). This is the only host species whose range largely encompasses the distribution of this parasite. Another important but less widely distributed host is *Anthophora occidentalis* Cresson. It has been recorded as a host of *H. minutipennis* in Colorado by Mickel (1928a), and in Wyoming, Idaho and Utah by Bohart and Selander (1955). The third known host is *Anthophora abrupta* Say which was reported in association with the meloid from several localities in Missouri by Riley (1877) and Rau (1926). Of possible significance is the apparent restriction of Pacific Coast populations of *H. minutipennis* to the well defined and similarly restricted subspecies *A. b. stanfordiana*. Also, and perhaps associated with this host specificity, are considerable differences in biology from those populations reported on by Bohart and Selander (1955).

Based on the evidence now available it appears advisable to restrict the subspecific name *H. m. occidentalis* Linsley to those populations occurring in Central and Coastal California. A considerable number of additional adult and larval collections will be necessary before a clear picture of subspecific relationships can be determined.

Hornia boharti Linsley

An examination of the types of *H. boharti* Linsley has revealed the presence of inconspicuous but distinct tarsal spines. In the male, each spine is small, slender and hyaline and reaches a point less than one-half the distance from the base to the apex of the claw. On some claws the spines appear to be absent while rarely they are longer than usual. The spines of the tarsal claws of females are considerably shorter and more frequently appear to be absent.

Hornia mexicana Dugès

Linsley (1942) pointed out that there is little basis in the literature for the separation of *Hornia neomexicana* (Cockerell) and *H. mexicana* Dugès, the drawings of the latter being inaccurate and inconsistent in those very structures which have been used to distinguish the two species. Also Mickel (1929) demonstrated, in a study of the type material of *H. gigantea* Wellman, *Leonidia anthophorae* Mickel and *H. neomexicana* (Cockerell), that the characters by which they had been separated were intraspecifically variable and synonymized the three species under the name *H. neomexicana*. Certain of these variable structures, particularly the antennae and maxillary palpi, were those which were inconsistently figured for *H. mexicana* and also were used to separate *H. neomexicana* from *H. mexicana* (Cockerell, 1899). However, in the absence of material with which to make direct comparisons and since there were differences in coloration, a wide gap in distribution, and Dugès' (1889) colored plate suggested a different insect, Linsley (1942) thought it inadvisable to synonymize the two species at that time. The recent acquisition of a large collection of *Hornia* from San Cristobal Las Casas, Chiapas, Mexico, permits further speculation on the relationships of *H. mexicana* and *H. neomexicana*. Unfortunately this collection site is also separated by a considerable distance from the type locality of *H. mexicana* (Hacienda Tupataro, Guanajuato, Mexico). Nevertheless a comparison of Chiapas material with specimens of *H. neomexicana* from near Carlsbad, New Mexico strongly suggests that there is only a single species involved.

The antennae of meloids commonly exhibit structural variations which have been used to recognize genera and species and these appear to be diagnostic at the species level in the genus *Hornia*. The antennae of *H. minutipennis* Riley and *H. boharti* Linsley are always 11-segmented. By contrast, there is a tendency for ankylosis of the terminal antennal segments in the other species of the genus. In Mickel's (1929) study of *H. neomexicana* he found that 14 specimens had 11-segmented antennae, 35 had 10 segments, and 10 specimens had 10 segments in the antennae but the last segment had a remnant of a suture indicating an eleventh segment. An examination of a population of *H. neomexicana* from Loving, Eddy County, New Mexico gave the following similar results: 6 with 11-segmented antennae, 25 with 10 segments, 19 with a partial fusion of the tenth and eleventh segments on one or both antennae, and 1 specimen with 10 segments on both antennae but with a partial fusion of the ninth and tenth segments on one side. In most specimens with 10-segmented antennae the ulti-

[2]A small collection of *H. minutipennis* was made from the cells of *Anthophora bomboides neomexicana* Cockerell near Blanco's Corral, White Mountains, Mono County, California, on June 23, 1953. At this time a few bees had emerged, and four females, three depauperate males, and eggs and first instar larvae of *H. minutipennis* were collected.

mate and penultimate segments are subequal. In most other situations the terminal segment is distinctly longer than the penultimate segment. Cockerell (1899) described *Leonia neomexicana* (= *Hornia neomexicana*) as having 10-segmented antennae with the last two segments similar. This he contrasted to Dugès (1889) description of *Leonia rileyi* (= *Hornia mexicana*) in which the antennae were 10-segmented but the tenth longer than the ninth. In this same description Dugès notes that segments 5 and 6, 7 and 8 have the tendency to become connate into a single joint. Furthermore, in the illustrations accompanying this description the right antenna is clearly 10-segmented while the left antenna appears to have a suture near the apex of the tenth segment. The antennae of the specimens from Chiapas are as follows: 132 specimens with 10-segmented antennae, 34 with 10 segments but with a partial fusion between the ninth and tenth segments on one or both antennae, 1 with 10 segments on both antennae but with the remnant of a suture on one antenna indicating the possibility of an eleventh segment, and 1 specimen in which there is a partial fusion of segments 4 and 5, and 8, 9 and 10 on one antenna and between segments 4 and 5, 6 and 7, and 8, 9 and 10 on the other. In addition, there is sufficient variation in relative size and shape of the antennal segments to fit either the descriptions of *H. neomexicana* or *H. mexicana*. Some figures of the antenna of *H. mexicana* show the second and third antennal segments as being strongly produced laterally and this characteristic has been used by both Cockerell (1899) and Linsley (1942) to separate this species from *neomexicana* in their keys. As Dugès had specimens of *H. minutipennis*, which he compared with the two specimens of *H. mexicana*, it is surprising that this presumably marked difference was not noted in his description of *H. mexicana* or his comparisons of the two species. It appears more reasonable to assume that the minor lateral projections of these segments have been overemphasized in illustration.

The coloration of *H. mexicana* as described and figured by Dugès (1889) can be examined further in relation to the large series of specimens from New Mexico and southern Mexico. The color of the elytra of *H. mexicana* was described as testaceous and that of *H. neomexicana* as fulvous. In both of the series of specimens mentioned above are individuals whose elytra are somewhat more yellowish or reddish than the average condition for either series. Similarly, the integumental pigmentation is variable in both series. Those from New Mexico commonly have some ferrugineous pigmentation but only a few specimens from southern Mexico have some ferrugineous pigmentation. In general, it is females which are the most lightly pigmented.

From a consideration of the evidence available there appears to be little reason for continuing to recognize *H. mexicana* Dugès and *H. neomexicana* (Cockerell) as two valid species and therefore the latter name is here reduced to a subspecific status. However, as noted below, populations from the southwestern United States and southern Mexico are subspecifically distinct from each other. Until additional material is available from Guanajuato, it will be impossible to determine whether the nominate subspecies is the same as the northern or southern populations or represents even another segregate of this widely distributed species.

TABLE II

Associated Parasites and Predators of *Anthophora occidentalis* near Loving, New Mexico

	Locality No. 1		Locality No. 2		Locality No. 3	
	Number of Cells	Percent of Total	Number of Cells	Percent of Total	Number of Cells	Percent of Total
Cells examined	391	100 0	81	100 0	64	100 0
Living *Anthophora*	277	70 8	43	53 1	32	50 0
Anthophora killed by mold	11	2 8	33	40 7	20	31 2
Hornia m. neomexicana	74	18 9	—	—	9	14 1
Nemognatha piazata	—	—	1	1 2	—	—
Xeromelecta californica	22	5 7	2	2 5	—	—
Monodontomerus montivagus	4	1 0	—	—	—	—
Dasymutilla dugesii	—	—	—	—	3	4 7
Bombyliid fly	3	8	2	2 5	—	—

Hornia mexicana neomexicana (Cockerell), new status

Observations on the habits of *Anthophora occidentalis* Cresson, its principal parasite *H. m. neomexicana*, and other associated species, were made at several localities near Loving, Eddy County, New Mexico, in 1945 and 1956. Six nesting aggregations of this species were found and samples of bee cells were collected from three of them (Table II). These data permit comparisons with those of Mickel (1928b) and Porter (1951) as well as with the less specific observations

of Hungerford and Williams (1912) and Long (1925) on the same bee species.

The nesting sites of *A. occidentalis* were found in a number of situations. Three were located in vertical banks along the Black River or in the banks of deep irrigation ditches. Another was in the walls of an adobe house near a small irrigation ditch. A fifth was in the walls of a large cave near the Black River and the last was in the walls of an old dry well near the Pecos River. The species shows a definite preference for cavities in otherwise vertical surfaces. In the cliffs, the bees commonly excavated their burrows in overhung or partially eroded portions and in one cliff they were within animal burrows almost three feet from the cliff's outer surface. Each burrow of *A. occidentalis* has a turret at the entrance which projects out for 12–16 mm. and then turns down (90 percent) or upward (10 percent) for from 2.5 to 5 cm. The turret characteristically has a partial split in the outer surface which is fashioned by the female at the time of construction and is not the result of cracking, as has been suggested by Hungerford and Williams (1912). The internal measurements of a number of turrets varied from about 9 to 9.5 mm. The burrow, which is excavated by the use of water, penetrates the soil horizontally for from 10–14 cm. and then turns vertically for varying distances. From one to four vertical shafts are constructed and usually contain from three to four cells each. The external measurements of these cells averaged 16 by 27 mm. and the internal measurements were 10 by 19 mm. These measurements are somewhat larger than those found by Porter (1951) in Texas. Completed burrows are plugged at the surface.

Limited data on the pupal period and seasonal appearance of adults of *A. occidentalis* were gathered. The samples from Localities 2 and 3 (Table II) were collected on April 14 and at this time only prepupal bees were found. The samples from Locality 1 were taken between April 27 and May 1 and 45 of the 277 *Anthophora* were pupae. However, the first two localities sampled were in north-facing cliffs while the exposure of the third was to the southwest. Twenty-three bee larvae from these samples were kept individually to determine the pupal stage. Of these, 14 were males which completed the pupal stage in 22 to 25 days (average 22.8) and 9 were females with a pupal stage of 21 to 26 days (average 23.3). The first emergence was on May 17 at which time a small number of males and females were collected. From these few observations it is not clear that *A. occidentalis* is proterandrous as reported by Porter (1951).

Hornia m. neomexicana (Cockerell) was the most abundant insect parasite associated with *A. occidentalis* in two of the three localities sampled. *Hornia* was also present in the adobe house locality but absent in the cave and well populations which were small. The nine *Hornia* collected from Locality 3 were in the larval stage on April 14. Of those collected from April 27 to May 1 at Locality 1, 8 were in the larval stage, 50 were pupae and 4 were adult males in unopened cells. The eight larvae later transformed to the pupal stage. The first female emerged and copulated on May 4.

In the field, males commonly mate with females from the same cell series or may occasionally be found walking over the cliff surface in search of burrows containing unfertilized females. On May 23, at Locality 1, a total of thirty males and one female were found with their heads in small circular holes cut in the surface plugs of the burrows. More than one-half of these males had copulated previously as evidenced by their shrunken abdomens. No males were found crawling on the face of the cliff but one was found in a spider's web. Several burrows, which had circular holes in the entrance plugs, were excavated without finding any males in the burrows. Others were removed from cells where they were in copulation with females. Also a few *Hornia* pupae but no over-wintering larvae were excavated. Although *H. m. neomexicana* pupates shortly before emergence as does the related species, *H. boharti* Linsley, it has a one- rather than two-year life cycle and appears to lack the resistant larval stage of the latter species. On June 6, which was extremely windy, no *Hornia* were found with their heads in the holes in the plugs but six males and two females were found dead in the talus at the base of the cliff. On June 9, eight males were taken with their heads in entrance plugs and two others were climbing over the bank in the shade.

Two females of *H. m. neomexicana* copulated in the laboratory and daily oviposition was recorded. Although the numbers of eggs, 362 and 365, are considerably less than the 600 to 700 eggs reported by Porter (1951), the pattern of oviposition is of interest. One female laid 235 eggs in the first 24 hours and then 45, 25, 30, 14, 11 and 5 on succeeding days. The other laid 3 eggs on the first day followed by 117, 74, 26, 49, 18, 33, 23, 12, 2, 0, 5, 1, 0 and 1. Although the second female produced eggs for a two-weeks' period this is strikingly less than the six weeks reported for *H. minutipennis occidentalis* Linsley and the two months' period of *H. boharti* Linsley by Linsley and MacSwain (1942). It is possible, in view of the small numbers of eggs, that the two *H. m. neomexicana* females were abnormal. One female lived only 18 days and the other 19.

The incubation period of more than two hundred eggs ranged from 20 to 22 days. This is similar to *H. minutipennis* as recorded by Linsley and MacSwain (1942) and Bohart and Selander (1955) but only one-half the period of *H. boharti* (Linsley and MacSwain, 1942).

Monodontomerus montivagus Ashmead occurred

in four of the cells from Locality 1. Each cell contained both male and female chalcids in the following numbers: 1 male, 17 females; 2 males, 24 females; 2 males, 25 females; and 1 male, 30 females.

Xeromelecta californica (Cresson) was reared in the small numbers which appear to be usual for this species. The pupal stage was determined for two males of *X. californica* as 19 and 22 days.

In addition to the species listed in Table II several other insects were recovered from the cells of *A. occidentalis*. These were a single male of *Dasymutilla fulvohirta* (Cresson), a pupa of an unidentified ptinid beetle, and dermestids and psocids which were not identified.

Hornia mexicana blomi MacSwain, new subspecies[5]

Adult male.—Color of head, antennae, thorax, and legs black, abdomen dark brown to piceous, with narrow pale margins on tergites and sternites; integument clothed with moderately short, moderately dense, erect, coarse, black setae; setal length equal to or slightly longer than greatest width of antennal segments. *Antennae* ten-segmented. *Legs* with tarsal claws ferrugineous at base, piceous at apex, armed with a long, slender, inner spine which reaches at least to apical four-fifths of claw. Length 9–12 mm.

Adult female.—Color of head, antennae and thorax piceous to black, legs ferrugineous, abdomen dark brown. Length 9–11 mm.

Primary Larva.—Mandibles bearing six or seven inner teeth, four or five apical teeth complete, basal teeth weakly developed; maxillary palpi with third segment distinctly shorter than second segment. Length 1.8–2.1 mm.

Type locality.—San Cristobal las Casas, Chiapas, Mexico.

Host.—*Anthophora marginata* Smith.[6]

Types.—Holotype adult male (Calif. Acad. Sci., Entom.), allotype adult female (Calif. Acad. Sci., Entom.) and two hundred and seventeen paratypes (172 ♂♂, 45 ♀♀) from San Cristobal las Casas, Chiapas, Mexico, July 8–10, 1956, J. W. MacSwain collector. Paratypes deposited in the collections of the California Academy of Sciences, the California Insect Survey and the U. S. National Museum.

Populations of this subspecies are readily separated from those of *H. m. neomexicana* in the adult and larval instars. The adults of *H. m. blomi* are darker, have longer body setae and longer setae of the tarsal claws and the tendency for ankylosis of the terminal antennal segments is more advanced. The larvae have more teeth in the mandibles and the third segment of the maxillary palpus is shorter rather than longer than the second segment as is the case in *H. m. neomexicana*.

The host of *H. m. blomi*, *Anthophora* (*Amegilla*) *marginata* Smith, is of interest for several reasons. This bee was originally described from Mexico by Smith (1854) and was later recorded from Orizaba, Vera Cruz, Mexico, by Dours (1870), from Santa Fé, New Mexico (as *Podalirius cleomis* Cockerell) by Cockerell (1896) and from Arizona by Michener (1951). Although this species occurs within the range of all of the subspecies of *Hornia mexicana* it appears to be uncommon in the southwestern United States and Cockerell (1896) considered the species (as *P. cleomis*) to represent a northward extension of a neotropical type. It is also the only species of the subgenus *Amegilla* to have been associated with *Hornia*, although several other species occur commonly throughout most of the range of the other *Hornia* species. A few observations on the habits of *A. marginata* and its parasites were made at San Cristobal las Casas between July 8 and 10 and July 27 to 31, 1956.[6]

On July 8, a few *Anthophora marginata* were found in the adobe walls of several buildings a few blocks from the northern edge of San Cristobal las Casas. Two males of *Hornia mexicana blomi* were collected at the same time. Later the same day, an adobe house on the northern edge of town was found which had suffered considerable damage from the burrowing activities of this bee. Although only a moderate number of *Anthophora* males and females were flying around this building, 108 males and 20 females of *Hornia m. blomi* were taken. The beetles were captured walking on the surface during cloudy periods or were extracted from within burrows or cracks between the adobe bricks with forceps. Additional observations and collections during the next two days revealed that the burrows were very shallow and that the emergence of the bees had just started. One bee cell at the surface was opened and contained a living bee pupa. However, adult activity of the *Hornia* was well advanced and many dead males and a few dead females were collected along with a greater number of living individuals. One dead female with her eggs was taken from a cavity near the surface and a few other eggs but no larvae were also found. When the house was revisited on July 27, a single living depauperate male *Hornia* was found and many dead males and a few females were on the ground at the base of the walls. A number of larvae were found within cavities or walking on the surface. At this time most of the *Anthophora* were flying around the walls investigating cracks and crevices and only a few were provisioning. As the house was not occupied and the owner could not be located no further

[5]This subspecies is named in honor of Mr. Frans Blom, who did much to facilitate this and other studies in Chiapas, Mexico.

[6]Identified by P. H. Timberlake.

[6]Donald D. Linsdale assisted in making the following observations.

observations were made at this location. On July 30 another but less heavily infested locality was discovered in the north-facing wall of a mill some distance north of town. The owner, Señor Cansino, kindly allowed us to cut out small sections of this wall. Here, several bees were observed constructing their burrows and, although no bees could be found visiting a number of nearby water sources, the finely grained excavated material was moist. It was verified that the burrows were extremely shallow and usually consisted of only one or two cells. One burrow, which was excavated, was 3.2 centimeters to the end of the single cell. As in other known species of *Anthophora* the cells were formed within a larger cavity, had a thick inner lining of wax and were provisioned with a small amount of pollen covered with a larger amount of liquid which had the strong fermented odor characteristic of other *Anthophora* species. A number of cells had external measurements of about 9 and 15 mm. and internal measurements of 7.5 and 12 mm. Several different pollen sources were being used by the bees and the principal one was determined as *Cuphea aquipetala* Cav.[6] At this same time a few females were observed carrying large numbers of larvae of *Hornia* while most individuals had only a few or none. A count of the larvae on four heavily infested females was 20, 29, 37 and 131 larvae. Most of the larvae on the last female were located on the hind legs and the scopal areas were a solid mass of larvae. It was apparent in both localities studied that the *Hornia* was infesting a large percentage of the cells of the host and perhaps more than fifty per cent were destroyed by this parasite. A few other parasites and inquilines were observed but they were uncommon. A bombyliid skin was found in one burrow and a number of cells were found infested with mites. In addition, a few adults of the chalcid parasite *Monodontomerus mexicanus* Gahan[7] were taken on the walls as were a few unidentified dermestids.

[6]Identified by Mrs. Helen K. Sharsmith, University of California Herbarium.

[7]Identified by B. D. Burks, U. S. National Museum.

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HETEROPTERA: ARADIDAE. INSECTS OF MICRONESIA, by RYUICHI MATSUDA and ROBERT L. USINGER. Vol. 7, No. 3, pp. 117–172, 1956. Illus. Bernice P. Bishop Museum, Honolulu, Hawaii. Price $1.50.

Forty species of Aradidae belonging to 11 genera are recorded from Micronesia. Distribution shown for the different island groups indicates that 29 species are one-island endemics. Palau, with 21 of the 40 known species, seems to support the most numerous and diverse aradid fauna. Four of the genera and 27 species are described as new and in view of the secretive habits of the flat bugs it seems likely that many additional species will be found as the faunas of the different islands become better known.

Only four species are known to occur outside Micronesia. Three of these are widely distributed in the Orient and the other is known from Samoa. In general, species relationships seem to be nearest the fauna of the Philippines and the islands of the southwestern Pacific. More specific information on faunal relations must await careful study of the aradids from these adjacent regions. Keys are provided for all taxa, new species are well illustrated and illustrations and descriptive material are provided for some of the previously described species. In all respects, the paper maintains the excellent standard of the series.

REECE I. SAILER.

OBSERVATIONS ON EGYPTIAN HYALOMMA TICKS (IXODOIDEA, IXODIDAE). 4. IDENTITY, DISTRIBUTION, AND HOSTS OF H. FRANCHINII TONELLI-RONDELLI (NEW COMBINATION). SYSTEMATIC STATUS OF H. TUNESIACUM SC. & SC. AND ITS SUBSPECIES[1]

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ABSTRACT

Hyalomma (H.) franchinii (H. tunesiacum franchinii T.-R. 1932; = *H.* sp. no. 1 near *excavatum* of Hoogstraal, *olim*) is a valid species ranging across the littoral semi-desert from Tripolitania to the desert edge of the Nile Valley and also occurring in Sinai; notes are given for its identification. Its larvae and nymphs parasitize lizards throughout the year; adults feed and mate on domestic animals during the cooler months. *H. a. anatolicum* Koch 1844, *sensu* Schulze, *nec* Pomerantzev 1950 (= *H. tunesiacum* Schulze and Schlottke 1930, and its subspecies *turkmenicense* Oleney 1931 and *ganorai* T.-R. 1932; = *H. a. excavatum* Koch 1844, *sensu* Pomerantzev 1950; = *H.* sp. no. 2 near *excavatum* of Hoogstraal, *olim*), *H. t. pavlovskyi* Sc. & Sc. 1930 and *H. t. amurense* Schulze in Kratz 1940 are considered *nomina dubia*. These conclusions are based in large part on study of the Schulze collection, which contains cotype material of several of the forms discussed.

INTRODUCTION

Study of material in the collection of the late Professor Schulze, kindly loaned to us by Mr. Glen Kohls of the Rocky Mountain Laboratory, reveals that "*H.* sp. no. 1 near *excavatum*" of Hoogstraal (1956) is identical with *H. tunesiacum franchinii* Tonelli-Rondelli, 1932. The present report presents new data and briefly collates the available information concerning this species.

The systematic status of each of the other subspecies assigned by Kratz (1940) to *H. tunesiacum* Schulze and Schlottke is also investigated.

Hyalomma (Hyalomma) franchinii
Tonelli-Rondelli, 1932

(New Combination). The Northeast African Lizard Hyalomma.

Hyalomma tunesiacum franchinii n. sp., Tonelli-Rondelli, 1932, pp. 121–122; description of ♂ only; figs. (unnumbered) of ♂ dorsum, capitulum, anal area, coxa IV, spiracular plate; type locality Tauorga Oasis, Tripolitania, Libya; type material stated (page 120) to be deposited in the Institute of Colonial Pathology of the University of Modena and in the Civic Museum of Natural History of Milan.

Our 1957 correspondence with officials of the University of Modena (Professors M. Aloisi and F. Marzullo), with the Museum of Milan, and with the Institute of Parasitology of the University of Rome (Professor O. Starkoff) indicates that these specimens are not now present in their collections. Two males in the Schulze collection, presently housed at the Rocky Mountain Laboratory and loaned by Mr. Glen Kohls, bear the following label in Dr. Tonelli-Rondelli's handwriting: "*Hyalomma tunesiacum franchinii* Tonelli-Rondelli. Tauorga, Tripolitania, Camelli e pecore, Primavera, 1931." Since this is the same time and locality at which the originally described specimens were collected (Tonelli-Rondelli, 1932, p. 119) and since Tonelli-Rondelli (*op. cit.*, p. 120) states that she had sent specimens to Professor Schulze, it appears obvious that the two males now in the Rocky Mountain Laboratory are part of a cotype series, and apparently the only surviving sample from this group. We therefore designate one of these two males as a lectotype. These two specimens correspond exactly to *Hyalomma* sp. no. 1 near *excavatum* (Hoogstraal 1956, pp. 880–883).

Kratz (1940, p. 526) provided a diagnosis of *H. tunesiacum franchinii* and stated that types were in the "Zool. Museum Mailand". Delpy (1949, pp. 477 and 488), synonymized this form under *H. excavatum*, without reference to the type material, as also did Feldman-Muhsam (1954, p. 159) and Tendeiro (1956, p. 388).

Hyalomma species no. 1 near *excavatum*. Hoogstraal (1956, pp. 880–883, figs. 329–332) gave short notes on distribution, hosts, and biology and redescribed and illustrated both sexes. Hoogstraal and Kaiser (1958, pp. 7–12, figs. 1–5) reported parasitism of lizards by immature stages in nature and experimentally.

KNOWN DISTRIBUTION. EGYPT. *Western Desert Governorate:* Siwa Oasis, Salum, Bir Bosslanga near Salum, Mersa Matruh, El Alamein, El Hammam, El Amiriya, Wadi Natroun. *Giza Province:* Giza Pyramids, Giza, Kirdasa, Abu Rawash, El Mansuriya. *Sinai Governorate:* El Arish, St. Catherine's Monastery (5000 feet elevation). LIBYA. *Cyrenaica:* Gheminez. *Tripolitania:* Tauorga Oasis (type locality). This oasis is about 25 miles south of the Mediterranean coast a few miles east of 15° East longitude.

HOSTS OF ADULTS AND MONTHS OF COLLEC-

[1]Accepted for publication January 4, 1958. Research Report NM 52 08 03.10. The opinions and assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

TION.[2] EGYPT. Camels: 12♂ ♂ (January), 13♂ ♂, 2♀ ♀ (March), 2♂ ♂ (May), 4♂ ♂, 2♀ ♀ (October). Cattle: 3♂ ♂, 10♀ ♀ (January). Sheep: 8♂ ♂, 1♀ (October). LIBYA. Land tortoise: 1♂ (October). "Camels and sheep, several ♂ ♂ (Spring-time)" (from Tonelli-Rondelli, 1932, and from her specimen labels).

HOSTS OF IMMATURE STAGES. These have been reported by Hoogstraal and Kaiser (1958) to be chiefly the lizard *Acanthodactylus boskianus asper* (Audouin), but to include also the lizards *Acanthodactylus s. scutellatus* (Audouin) and *Agama mutabilis* Merram, as well as the spiny mouse *Acomys russatus* (Wagner). Larvae and nymphs are found on lizards during all months of the year.

LIFE CYCLE. *H. franchinii* is a three-host tick. Its life cycle under laboratory conditions was reported by Hoogstraal and Kaiser (1958). Considerable additional data obtained during the past year merely confirm these details.

IDENTIFICATION. Beyond the description provided by Hoogstraal (1956, pp. 880–883) only the few following additional notes are necessary to identify and compare this distinctive species; the illustrations were repeated in Hoogstraal and Kaiser (1958) for greater clarity in reproduction.

Male: The typical shiny dark brown scutal color becomes more reddish brown in smaller specimens. Cervical grooves are short, wide, shallow, and smoothly rounded; they become shallower and fainter posterior of eye level. Punctations adjacent to lateral margins of scutum are more dense than on central dorsum. The parma is distinct or indistinct, usually the color of the scutum or paler, usually triangular, sometimes subrectangular and whitish. The two festoons bordering the midfestoon (parma) are not joined anteriorly by a slightly elevated ridge (pons) (this character is widely used for certain species by Russian workers). Adanal shields are strong with rectangular posterior margins that are usually slightly emarginate medially. Subanal shields vary from small to moderate size; they are elongate and the margins converge distally. Leg segments have more or less pronounced pale distal rings and dorsal enameling, the latter chiefly on the two posterior pairs.

Female: Two to four large, shallow punctations are scattered on the posterior half of the scutum; the scapulae and anterior margin of the scutum bear more numerous large punctations. Minute shallow punctations regularly scattered over the scutum do not detract from its smooth appearance; these are more pronounced anteriorly. The cervical grooves are wide, smoothly rounded, converging to the level of the eyes and thence diverging as more shallow, indistinct linear depressions reaching to or almost to the posterior margins.

Note: These descriptions are only supplementary to those in Hoogstraal (1956, pp. 880–883).

[Hyalomma tunesiacum Schulze and Schlottke]

Hyalomma tunesiacum Schulze and Schlottke, 1930, p. 35, short, useless key description of ♂ only; locality Tunis.

H. t. tunesiacum Schulze and Schlottke; Kratz, 1940, pp. 523–525, figs. 3–4, new combination, diagnosis of ♂, type locality specified as Djesba, Tunisia, type depository as Zoological Museum, Berlin, type compared with specimens of both sexes from Biskara, Algeria, in Copenhagen Museum.

H. excavatum Koch, 1844, or *H. savignyi* (Gervais, 1844); Delpy, 1949, p. 488, new synonymy; type material not seen.

H. excavatum Koch, 1844; Feldman-Muhsam, 1954, p. 159, synonymy; type material not seen.

The Schulze collection in the Rocky Mountain Laboratory now contains only a single male of *H. tunesiacum* from Tunis. This is labelled Tunis, 1899; the rest of the writing is illegible. Mr. Kohls and we believe that this specimen may be a cotype of *H. tunesiacum*. It corresponds exactly to *H. anatolicum anatolicum* (*sensu* Schulze, not Pomerantzev).

[Hyalomma tunesiacum ganorai
Tonelli-Rondelli]

H. tunesiacum ganorai Tonelli-Rondelli, 1932, pp. 122–123, description of ♂ only; figs. (unnumbered) of ♂ scutum, capitulum, anal area, coxa IV, and spiracular plate; type locality Agordat, Eritrea. For depository of type material, the same remarks in the first two paragraphs under *H. franchinii* herein apply.

H. excavatum Koch, 1844; Tendeiro, 1956, p. 388, new synonymy.

The Schulze collection in the Rocky Mountain Laboratory contains two males bearing a label in Dr. Tonelli-Rondelli's handwriting "*H. tunesiacum ganorai* Tonelli-Rondelli, su cane e pecore, Agordat, Eritrea, Primavera, 1931." These were undoubtedly part of the cotype series sent to Professor Schulze (see second paragraph under *H. franchinii* above). They are typical specimens of *H. anatolicum anatolicum* (*sensu* Schulze, not Pomerantzev), and the original description and illustrations are also applicable to this form.

[Hyalomma tunesiacum pavlovskyi
Schulze and Schlottke]

H. detritum pavlovskyi Schulze and Schlottke, 1930, p. 36, short, useless key description of ♂ only; distribution Caucasus.

H. pavlovskyi; Olenev, 1931B, p. 100, new combination, included in key to Russian ticks but not further described.

H. tunesiacum pavlovskyi Schulze and Schlottke; Kratz, 1940, p. 524, new combination, diagnosis of ♂; type locality specified as on the River Araks, Trancaucasia, type depository as Zoological Museum, Berlin.

H. excavatum Koch, 1844; Feldman-Muhsam, 1954, p. 159, new synonymy, type material not seen.

H. excavatum Koch; Tendeiro, 1956, p. 388 "following Feldman-Muhsam".

[2]Between January and April 1958, we took approximately 200 additional adults, almost half of which were greatly engorged females, on Libyan camels at Hammam, Western Desert, Egypt. In March at the same place 12 males and 26 females were also taken from donkeys.

Pomerantzev (1950) did not mention *pavlovskyi*. We consider the name to be a *nomen dubium*. A single male in the Schulze collection, which may possibly be the type, bears the following legible writing "Fluss Arak June 1905, Jan. 1, 1906, N. 87106. *H. aegyptium* (Type)" in addition to much more worn and illegible writing. This specimen conforms to *H. anatolicum* (or *H. a. anatolicum*) (*sensu* Schulze, not Pomerantzev), and not to *H. excavatum* of non-Soviet workers.

[Hyalomma tunesiacum turkmeniense Olenev]

Hyalomma turkmeniense Olenev, 1931A, pp. 130-131, short description of ♂, no locality. Olenev, 1931B, pp. 107-108, fig. 67, redescription and illustration of ♂ (in Russian); geographic range, Middle Asia, Turkmen S.S.R., Gassian-Kulinsky area.

Hyalomma tunesiacum turkmeniense Olenev; Kratz, 1940, p. 527, new combination, diagnosis of ♂, type specimen said to be in Zoological Museum of Academy of Science in Leningrad.

H. anatolicum excavatum Koch, 1844; Pomerantzev, 1950, p. 214, new synonymy.

H. excavatum Koch; Delpy, 1949, p. 488, new synonymy, type material not seen.

H. excavatum Koch; Feldman-Muhsam, 1954, p. 159, synonymy; type material not seen.

H. excavatum Koch; Tendeiro, 1956, p. 388, "following Feldman-Muhsam."

We accept contemporary Russian workers' synonymy (e.g., that of Pomerantzev) of this form; they supposedly have easy access to the type specimen(s) in the Leningrad Academy of Science. However, inasmuch as Pomerantzev (1950) considered *H. anatolicum excavatum* in the same sense as Schulze considered *H. anatolicum*, it follows that *H. turkmeniense* is a synonym of *H. anatolicum* (or *H. anatolicum anatolicum*) (*sensu* Schulze, not Pomerantzev) and it is NOT a synonym of *H. excavatum* in the non-Soviet sense, as stated by Delpy and by Feldman-Muhsam, who did not see the type material.

[Hyalomma tunesiacum amurense Schulze, in Kratz, 1940]

Hyalomma amurense P. Schulze; Olenev, 1931A, p. 134, no description, distribution as "USSR, Amurgebiet"; Olenev, 1931B, p. 100, merely included species in brief key to ticks of Russia.

Hyalomma tunesiacum amurense Schulze; Kratz, 1940, pp. 525-526, figs. 6-7, new combination, short descriptions and illustrations of ♂ and ♀ attributed to Schulze; distribution Central Amur; type (1♂) deposited in Zoological Museum, Breslau.

H. excavatum Koch, 1844; Delpy, 1949, p. 485, new synonymy, type material not seen.

Contemporary Russian workers have ignored this appelation and we consider it to be a *nomen dubium*, with no assurance that it is a synonym of *H. excavatum*. So far as we can ascertain, the few lines in Kratz (*loc. cit.*), attributed to Schulze, comprise the only alleged description of this so-called species or subspecies.

DISCUSSION AND CONCLUSIONS

Hyalomma franchinii Tonelli-Rondelli, 1932 (new combination) appears from presently available data to be a comparatively uncommon tick of Northeast Africa confined to oases, desert edge and littoral desert situations. Adults have been taken in nature only from autumn through winter to spring. We have experimentally fed both sexes to repletion on man. Mating, indicated by collections of females associated with males, occurs from October to March. Domestic animals, camels, cattle, and sheep are hosts of the adult stage, but a single male from a land tortoise (in Libya), considered in the light of immature-stage host predilection, suggests that tortoises may have been the preferred primitive hosts of adults. This possibility cannot be investigated in nature in Egypt where the only surviving tortoise populations are of small individuals confined to narrow stretches of wilderness at the eastern and western frontiers of the country. Immature stages infest lizards during all months of the year and less commonly feed on spiny mice. Evaluation of this species as a legitimate taxon is based on field collections noted above as well as on extensive laboratory rearing and breeding of approximately one hundred adults from immature stages collected in the field; its identity was determined by comparison of specimens obviously a part of the cotype series in the collection of the late Professor P. Schulze.

H. franchinii is so distinct that it cannot be confused with any other species once its critical morphological characters, especially the form and structure of the female genital aperture, are known. Although previously synonymized under *H. excavatum*, even by the workers who first suggested the diagnostic value of the female genital aperture, these errors were made only because the original and field-collected material were not studied or compared. We presently consider *H. excavatum* as part of a complex consisting of *excavatum*, *anatolicum*, and *lusitanicum*, all described by Koch, 1844. This complex will be elucidated in the forthcoming paper of the present series.

H. franchinii was originally described as a subspecies of *H. tunesiacum* Schulze and Schlottke; therefore it became pertinent for us to ascertain the systematic status of the various subspecies assigned to *H. tunesiacum* by Schulze's student Kratz (1940). From certain material appearing to be the entire or part of the individual type series in the poorly labelled Schulze collection it was determined that *H. tunesiacum* Sc. and Sc., *H. tunesiacum ganorai* Tonelli-Rondelli, and *H. tunesiacum turkmeniense* Olenev are identical with *H. anatolicum anatolicum* Koch (*sensu* Schulze, not Pomerantzev) and that they are not synonymous with *H. excavatum* (*sensu* Schulze, not Pomerantzev) as claimed by most contemporary non-Soviet workers. *H. tunesiacum amurense* Schulze and *H. t. pavlovskyi* Sc. and Sc. are considered to be *nomina dubia*.

ACKNOWLEDGMENTS

We are grateful to Mr. Glen Kohls for the privilege of studying material in the Schulze collection, and to Mr. Kohls and Dr. C. B. Philip for reviewing the manuscript. The courtesy of Professors M. Aloisi, F. Marzullo, O. Starkoff, and others in searching for Tonelli Rondelli type material in Italian institutions is thankfully acknowledged.

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THE USE OF LARVAEVORID MAGGOT DROP IN MEASURING TRENDS IN SPRUCE BUDWORM POPULATIONS[1]

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ABSTRACT

The method is based on the assumption that the number of maggots of a group of dipterous parasites falling on a unit area of ground will be an index of the spruce budworm populations on the tree above that area. An analysis of 2 years' data indicated considerable variation in budworm population between trees. Budworm distribution within trees was markedly correlated with crown level the top third having the most larvae and, indirectly, the most maggots. Crown length provided good stratification for expressing and estimating budworm larvae and fly maggot populations. An estimate of significant differences between populations can be determined not only for any 2 years within the same area but also for any two areas during the same period.

During the past 2 years studies have been carried on in the spruce-fir types in northern Minnesota to determine spruce budworm (*Choristoneura fumiferana* (Clem.)) population in a given area. Our approach has been that, if the percent of parasitism of full-grown spruce budworm larvae by certain dipterous species can be accurately determined, the number of larvaevorid maggots falling on a unit area of the ground will be an index of the spruce budworm population on the tree above that area. For example, if 20 percent of the budworm larvae in a given area are parasitized by this group of larvaevorids then there should be five times as many budworms per unit area as larvaevorids trapped on the same area.

Measurements of maggot drop were obtained from cone-shaped muslin and wire traps (Fig. 1) suspended beneath the crown of individual study trees. Each trap was an inverted cone with a base 2 square feet in area. Only balsam fir (*Abies balsamea* (L.) Mill.) was used in this study. Data on individual tree height, d.b.h., crown class, vigor, and crown length and width were recorded. When the first larvaevorid maggot drop was observed, the traps were examined every other day and all puparia removed. Data on spruce budworm populations and larvaevorid parasitism were also obtained from a different set of trees, which were cut down and from which all budworm larvae were removed and reared. These data were supplemented by regular collections made in nearby biological study plots.

The original hypothesis that these traps could be used to measure absolute budworm popula-

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[2]Maintained at St. Paul 1, Minn., by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of Minnesota.

tions could not be proven statistically because of the lack of sufficient data. The analysis of the data from the cut trees showed a wide intertree variation in numbers of budworm larvae per tree. On the basis of the six trees examined the mean number of budworm larvae was 3,520±917 (range: 1,203–6,926). The number of trees needed to obtain a standard error for 500 larvae at the 5-percent significance level would be 64.

These data did indicate that the cone traps could be used to compare trends in spruce budworm populations in any two areas (or 2 years). However, to obtain a reliable comparison the percent of parasitism by larvaevorids would be needed for each area (or each year). The following example will show why. If 10 percent of the budworm larvae in one area are parasitized and the larvaevorid drop for that area averaged three larvaevorids per foot of crown length, the budworm population is 10 x 3 or 30 budworm larvae per foot of crown length. If in a second area 20 percent of the budworm larvae are parasitized and the larvaevorid drop averages only one per foot of crown length, the budworm population is 5 x 1 or 5 larvae per foot. Hence, the budworm population in the first area is six times as large as that in the second area instead of three times as might be indicated by the larvaevorid drop.

Several interesting facts were apparent from a further analysis of these data. When populations were plotted over certain tree factors, such as crown length, crown width, crown length x crown width, and basal area of the crown projection, there was an apparent relationship between crown length and budworm population (Fig. 2A). Further analysis of these data showed that the relationship between number of larvae and crown length was much stronger in the basal third of the crown length. There was considerable variation in both the mid and top thirds as indicated by the smaller correlation coefficients (Fig. 2B). The regression lines for the top two-thirds did form interesting striations. These differences in the vertical distribution pattern in number of larvae may be difficult to explain. The scarcity of food at any level was not a factor. It might be expected that the top levels, which receive more light, may have more new shoots per unit area of crown length than the lower levels.

When data on the larvaevorids collected from cut trees were substituted for data on the budworm population, the same relationships were observed: the number of larvaevorids varied greatly between trees, and was closely related to crown length (Fig. 2C). Also the number of larvaevorids increased from basal third to top third (Fig. 2D). Here again significant correlation was obtained only in the basal third. However, the striations were again apparent.

The larvaevorid data from the cone traps were next compared with those from the cut trees (Fig. 2E). (As mentioned before, the same sets of trees were not used for the comparison.) The average number of larvaevorids per foot of crown length was used as a basis for comparison. The two trends drawn through these data were parallel, but the average number of larvaevorids per foot on the cut trees was much higher and more variable than the average per cone trap. Only the latter showed a correlation coefficient significant at the 5-percent level. These data,

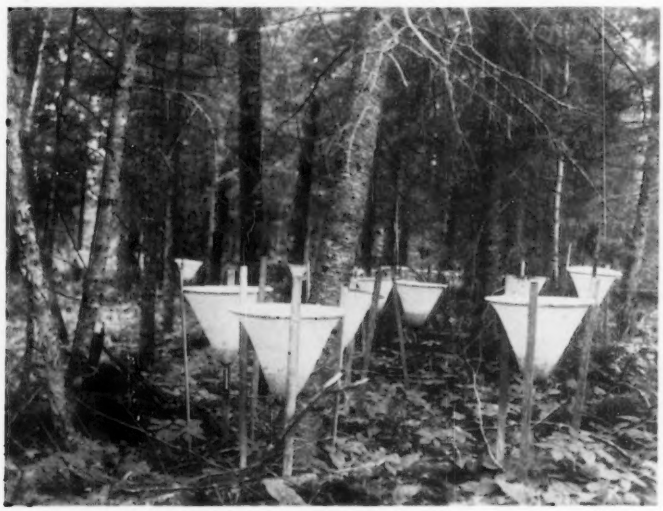

FIG. 1.—Cone traps used to collect larvaevorid maggots.

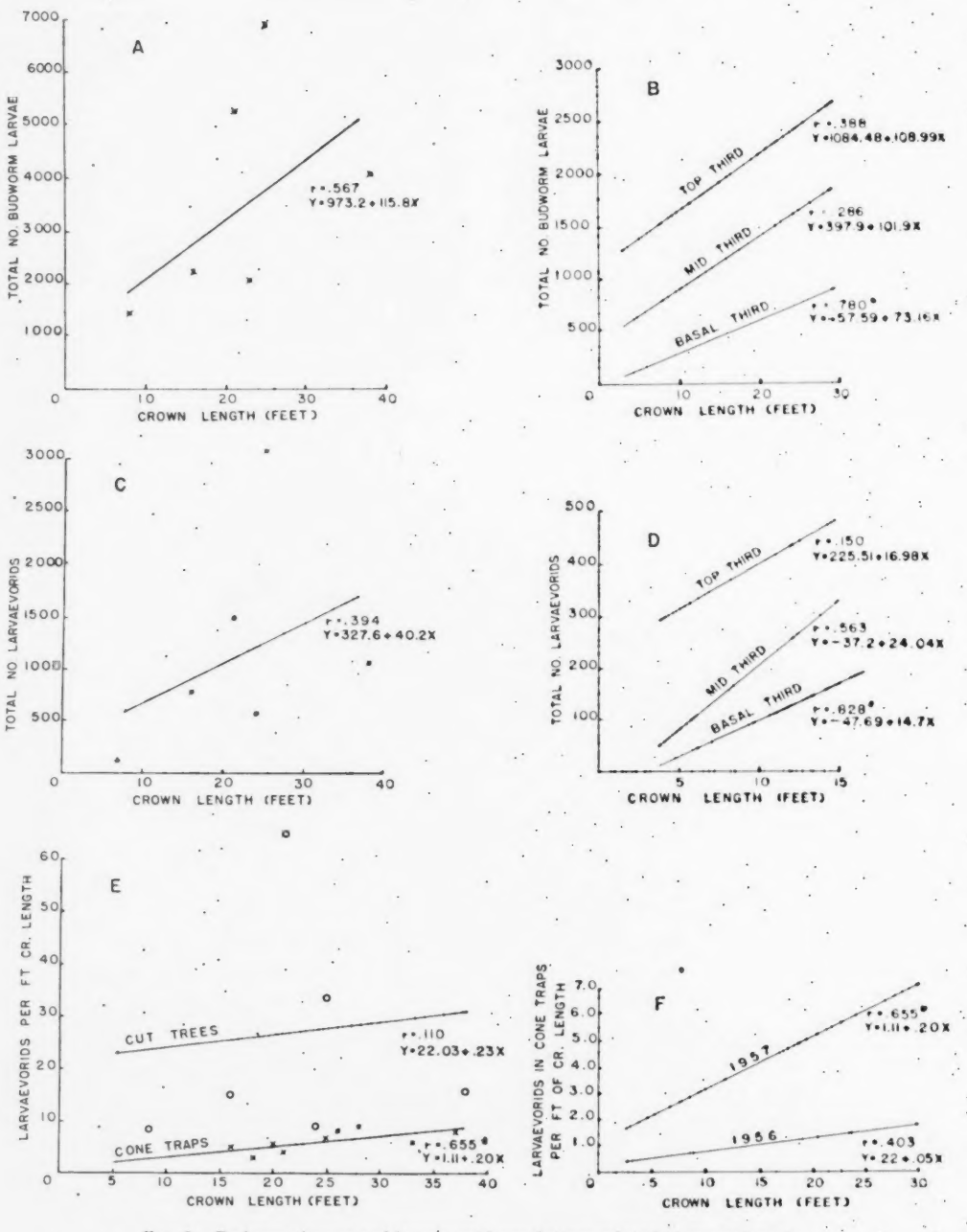

FIG. 2.—Budworm larvae and larvaevorid populations related to crown length:

A = Total number of budworm larvae from cut trees
B = Total number of budworm larvae from cut trees by crown thirds
C = Total number of larvaevorids from cut trees
D = Total number of larvaevorids from cut trees by crown thirds
E = Comparison of larvaevorids per foot of crown length for cut trees and for cone traps
F = Comparison of larvaevorids in cone traps per foot of crown length for 1956 and 1957

however, were not suitable for analysis on the basis of crown levels.

Cone trap data taken on these same trees in 1956 were compared next with the data for 1957 (Fig. 2F). Although the 1956 data were more variable, the comparison did indicate a significant increase in larvaevorid populations in 1957. An analysis based on paired data showed that these differences between the 2 years were highly significant ($t=5.163$ for 8df). There was no significant difference in larvaevorid drop between various sides of the same tree. Data showed that the drop was uniform at any point equidistant from the trunk of the tree. Neither was there a significant difference in drop along the radius of the crown projection. However, analysis of these data indicated that traps located halfway between the trunk and the periphery of the crown would give the most reliable estimate of the total larvaevorid drop.

In summarizing the above data the following was apparent. The wide variation in budworm population between trees would require a large number of trees to obtain an accurate estimate of the populations. The distribution of the larval population within trees was markedly correlated with crown level, the top third having the most larvae. Direct comparison between number of budworm larvae on the cut trees with the larvaevorid count in traps was not possible both because of insufficient data and because the two groups of data were collected from different trees. Crown length provided good stratification for expressing and estimating larvaevorid populations—the longer the crown the more larvaevorids. Even though cone trap counts may not agree with those from cut trees, they can be used to determine significant fluctuations in the trend of budworm populations based on larvaevorid parasitism. An estimate of significant differences between populations can be determined not only for any 2 years within the same area but for any two areas during the same period.

DIGESTIVE TRACT pH OF SIX SPECIES OF COLEOPTERA[1]

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ABSTRACT

The average pH for the six species ranged as follows: *Leptinotarsa decemlineata* (Say), 5.6 to 6.6; *Monocesta coryli* (Say), 5.7 to 7.3; *Leptura* sp., 5.5 to 7.1; *Osmoderma scabra* (Beauv.), 7.5 to 10.2; *Passalus cornutus* Fabr., 5.9 to 9.0; and *Cotnis nitida* (L.), 7.6 to 10.1. All measurements were made electrometrically using a one-drop glass electrode. The possibility of a relationship between food and digestive tract pH in Coleoptera is pointed out.

Swingle (1931) has reported on the pH for different regions of the digestive tracts of 21 species of Coleoptera; the measurements were made electrometrically using a modified quinhydrone electrode. Less complete data on digestive tract pH for five additional species of Coleoptera are included in the publications of Kruger (1933) and Staudenmayer and Stellwaag (1940). These results show a range in pH of 5.9 to 8.6 for the foregut, 5.0 to 9.6 for the midgut, and 5.4 to 8.2 for the hindgut of Coleoptera. Yushima and Ishii (1952) found values of 9.4 to 9.6 in the midgut of the rice stem borer, *Chilo simplex* Butler. The readings were made with color indicators on last-instar larvae which had been fed throughout most of their larval life on a synthetic diet.

Some differences in types of food normally consumed are found among the species of Coleoptera included in this study. The results reported are for two species feeding on the leaves of growing plants, one species feeding in solid wood underneath the bark of a log, two species feeding in a rotting log, and one species feeding on organic matter in the soil.

METHOD

The insect specimens were collected in their natural habitat, brought into the laboratory, and pH determinations made as soon as was feasible. Usually the readings could be completed within a few hours after collection of the specimens, but the insects were given appropriate food and living conditions in the event they had to be kept overnight. The pH was determined electrometrically with a one-drop, open glass electrode in combination with a calomel. Other details of procedure and the techniques employed in dissecting the insect specimens and removing the samples have been described (Grayson 1951 and 1955).

[1]Accepted for publication April 3, 1958.

RESULTS AND DISCUSSION

The results are presented in figures 1 and 2. The values shown for each region of the digestive tract is the average pH, plus or minus the standard error of the mean. The number of individual readings, from which these averages were obtained, were as follows: the larva of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), 11 to 16; the larva of the larger elm leaf beetle, *Monocesta coryli* (Say), 13; the larva of the cerambycid, *Leptura* sp., 9 to 10; the larva of the scarabid, *Osmoderma scabra* (Beauv.), 9; the adult of the passalid, *Passalus cornutus* Fab., 13 to 17; and the larva of the green June beetle, *Cotinis nitida* (L.), 17 to 19.

The larvae of *L. decemlineata* and *M. coryli* were collected from the leaves of their appropriate host plants. Most of the pH values obtained were slightly to moderately acid, and they varied within rather narrow limits throughout the digestive tract. The pH, 5.9 to 6.6, found in this study for the midgut of *L. decemlineata* is in rather poor agreement with the value of 5.0 listed by Kruger (1933).

The larvae of *Leptura* sp. were collected from rather solid wood underneath the bark of a log. The pH values obtained were neutral to moderately acid; these are in fair agreement with those reported by Swingle (1931) for Cerambycidae, except for the hindgut. However, such a comparison may not be valid because different species, or even genera, may be involved.

The larvae of *O. scabra*, and the adults of *P. cornutus*, were collected from a log in an advanced

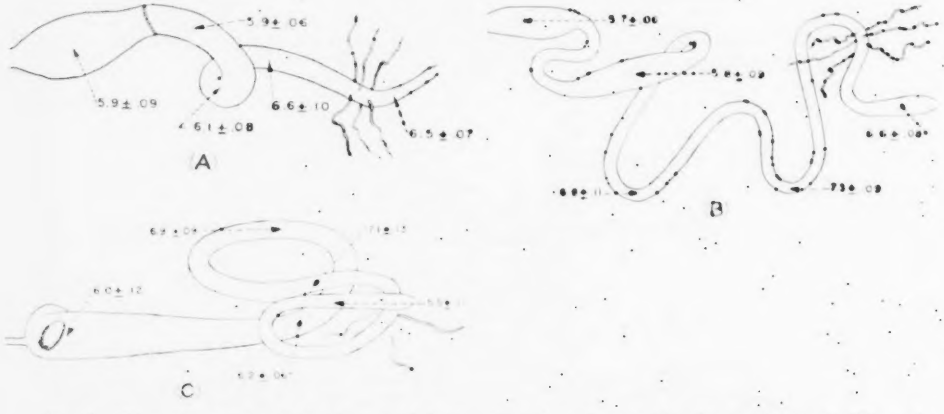

FIG. 1.—Digestive tracts of the larvae of *Leptinotarsa decemlineata* (A), *Monocesta coryli* (B), and *Leptura* sp. (C), showing pH in the approximate regions indicated. Foregut at left in each case, hindgut at right.

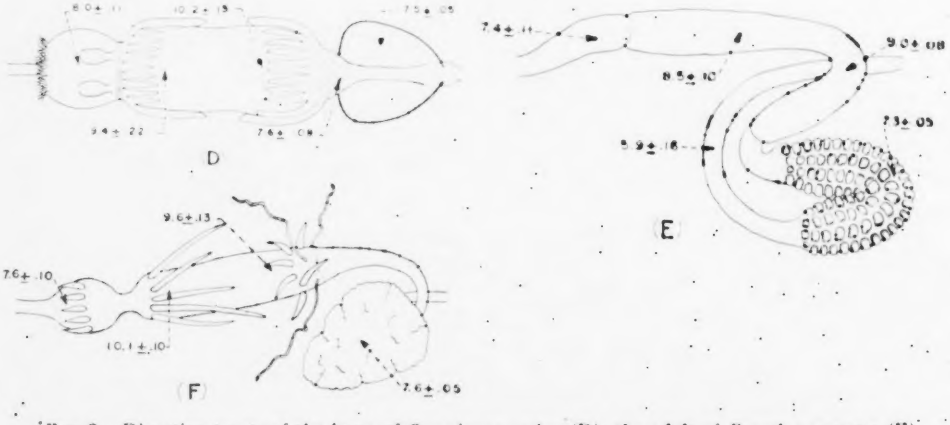

FIG. 2.—Digestive tracts of the larva of *Osmoderma scabra* (D), the adult of *Passalus cornutus* (E), and the larva of *Cotinis nitida* (F), showing pH in the approximate regions indicated. Foregut at left in each case, hindgut at right.

stage of decay. The pH values varied over a wide range from slightly acid to highly alkaline; except for the foregut, those found for *P. cornutus* are in fair agreement with the corresponding values reported by Swingle (1931).

The larvae of *C. nitida* were collected from soil where, presumably, they had been feeding on the organic matter present. The pH found in the different regions of the digestive tract ranged from slightly alkaline to highly alkaline.

The writer realizes the limitations of attempting to correlate acidity-alkalinity in the alimentary canal of insects with type of food consumed, taxonomy, or other criteria. However, in analyzing the available data on pH in the digestive tract of Coleoptera (Kruger 1933, Staudenmayer & Stellwaag 1940, Swingle 1931, and the data presented in this paper), it would appear that those species feeding on decaying organic matter have a medium to strong alkaline reaction in the midgut; whereas those feeding on living plant or animal tissue, grain products, or solid wood have a slightly alkaline to acid reaction in the midgut. This might indicate a relationship between food normally consumed and pH in the midgut of Coleoptera. A similar relationship for Diptera has been suggested by Grayson (1955); whereas, conversely, Waterhouse (1949) has generalized that midgut alkalinity is characteristic of the order Lepidoptera rather than being dependent upon feeding habits.

In postulating the above relationship, published pH values for the midgut of *Chilo simplex* (Yushima and Ishii 1952) were excluded from consideration because the larvae were reared on a synthetic diet which was likely different from their natural food.

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THE PHYLOGENY AND CLASSIFICATION OF THE NORTH AMERICAN GENERA OF THE SUBORDER TUBULIFERA (THYSANOPTERA), by Lewis J. Stannard, Jr. Illinois Biological Monographs, no. 25, 1957. v+200 pp. The University of Illinois Press, Urbana. $2.50 paper, $3.50 cloth.

Although this work does a considerable service in meeting the need for more usable aids to identification in Tubulifera, its major contribution is the first original arrangement of the group as a whole that has been presented since Priesner's Die Thysanopteren Europas.

It is probably to show the importance Stannard attaches to phylogeny that this word comes first in the title, as the first and larger part of the paper is devoted to classification. Following a short introduction and notes on habits, there are several pages on morphology that are invaluable for the inclusion of the many new terms and characteristics not explained in previous works in English on thrips morphology. A glossary would have been helpful, but the illustrations at the end of the paper leave little to be desired in the way of explanation.

In the section on classification, comprising a key to genera and a treatment of each within the two subfamilies recognized, Stannard's adherence to qualitative in preference to quantitative characteristics not only makes the key more workable, but also provides a sounder basis for the separation of genera. The key is far the best I have used in this group, with all due respect to the formidable accomplishment represented by Priesner's Genera Thysanopterorum. The chart of characteristics of difficult genera is an excellent device.

The treatment of each genus is a synonymy, characterization, discussion of relationships, species list, and occasionally a key to species. Although brief, the characterizations are more satisfactory than complete generic descriptions often are. Stannard does not indicate in the species lists which combinations are new and which may not represent his own opinion, but the lists will nonetheless be useful, and the keys even more so. The rejection of seven available names in favor of a name proposed to replace a senior homonym (*flavipes* (Jones) in *Haplothrips*, p. 51) is difficult to understand, as inadvertence could not account for so many, and the disregard for priority otherwise implied is contrary to his interpretations of nomenclature anywhere else.

It is more difficult to evaluate the section on phylogeny, but insofar as I am acquainted with the group, I find the scheme of relationships plausible. The jump to Tubulifera from Heliothripinae takes in a wide gap, but other groups of Terebrantia have even less in common with Tubulifera. Below the subfamily level, Stannard places genera in "lines" and "spurs," an arrangement with much logic, but extremely difficult to visualize without a chart or diagram. The "legalistic involvements in the International Rules of Nomenclature," he avoids by not assigning genera to definite intermediate categories, however, are minimal in comparison to those created by his drastic lumping of genera. Many of the new combinations are unlikely to be accepted by other thysanopterists, for if there is intergradation among the groups in question, there are also clear lines of relationship for which names are useful. There is also the need, as the author points out in not accepting *Leptogastrothrips*, to see critical specimens for one's self in order to judge whether the change is an improvement.

Kellie O'Neill

THE EFFECT OF INOSITOL ON GROWTH, SURVIVAL, AND MATURATION IN PERIPLANETA AMERICANA (L.)[1,2]

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ABSTRACT

American cockroaches reared on diets deficient in inositol appeared to develop normally for the first 50 days. Thirty days later, however, they weighed only one-third as much as those receiving inositol, and at 270 days their weight was less than one-half that of the controls; also, they showed 75% mortality and only 3% maturation of survivors, as compared to 13% mortality and 78% maturation in colonies receiving inositol. Diets containing 2500, 1000, 500, and 100 mg. of inositol per kg. were equally effective in supporting growth and development, and thus the critical level is below 100 mg./kg.—possibly in the range of the true vitamins.

Meso-inositol, also termed i-inositol, is one of nine possible isomers of 1, 2, 3, 4, 5, 6-cyclohexanehexol and the only one known to possess physiological activity. It is commonly found in animal and plant tissues, occurring as methyl and phosphoric acid derivatives and also in combination with phospholipids (West and Todd 1952). Customarily it is grouped with the B vitamins, although its principal role is thought to be that of a structural component rather than a metabolic catalyst, since it is found in such high concentrations and is not a part of any enzymatic cofactor (Wooster and Blanck 1956). It has been shown to function as a lipotrophic agent in man and other high animals (West and Todd 1952), and also appears to exert some role in carbohydrate metabolism, acting as a limited reserve for muscle activity (Wooster and Blanck 1956). Although the nutritional role of inositol is rather poorly defined, it has been reported as a requirement for yeast, fungi, and several vertebrates (West and Todd 1952).

In insect nutrition the role of inositol is even more obscure. It has never been shown to be an absolute requirement for any species (Lipke and Fraenkel 1956), and, partially as a consequence of this, very little is known concerning its utilization by the insect.

Those insects which have been shown not to require inositol in their diets are: *Silvanus surinamensis*, *Lasioderma serricorne*, *Sitodrepa panicea* (Fraenkel and Blewett 1943a, 1943b); *Tenebrio molitor* (Fraenkel *et al.* 1950); *Tineola bisselliella* (Frankel and Blewett 1946a); *Ephestia elutella*, *Ephestia cantella*, and *Plodia interpunctella* (Fraenkel and Blewett 1946b); *Blattella germanica* (Noland *et al.* 1949); *Culex molestus* (Lichtenstein 1948); *Drosophila melanogaster* (Schultz *et al.* 1946).

There have been several instances, however, where inositol seemed to favor growth to a small but measurable degree. Both *Tribolium confusum* and *Ptinus tectus* grew slightly better when the diet included inositol (Fraenkel and Blewett 1943b). It also appeared to have some nutritional value in the case of *Ephestia kuehniella* (Fraenkel and Blewett 1946b), although in this instance, also, the effect was not pronounced.

From the studies that have been made, it is apparent that inositol is not a dietary requirement for insects in general. However, this does not mean that the metabolism of the insect is independent of inositol nor does it preclude the possibility that it is an essential component of the diet of other species.

The present study is a precursor of biochemical research involving the utilization of various dietary components by the American cockroach, *Periplaneta americana* (L). For purposes of the study it was necessary to determine the nutritional value of inositol for this particular species.

METHODS AND MATERIALS

Diet Preparation.—The inositol-free diet used in this study had the following composition:

Dextrose U.S.P. (Fisher)	314 gm./kg.
Vitamin-Free Casein (G.B.I.)	300
Non-nutritive fiber (G.B.I.)	300
Linseed Oil—Raw (Dutch Boy)	30
Wesson Salt Mixture (G.B.I.)	40
Cholesterol C. P. (Fisher)	10
Choline Chloride (Fisher)	4
Para-amino-benzoic acid C.P. (Fisher)	300 mg./kg.
Nicotinic Acid U.S.P. (Fisher)	100
Thiamine Hydrochloride U.S.P. (Fisher)	70
Calcium Pantothenate (Eastman Kodak)	40
Pyridoxine Hydrochloride (G.B.I.)	18
Riboflavin U.S.P. (Fisher)	18
D L Methionine (Interchemical Corp.)	18
Folic Acid (G.B.I.)	6
Biotin (G.B.I.)	6

The inositol-containing diets (VI100, VI500, VI1000 and VI2500) were prepared by adding

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[2]A portion of this work was supported by the Thomas J. Headlee Research Fellowship.

100, 500, 1000, and 2500 mg./kg. of inositol, respectively, to the basic diet.

The dextrose, fiber, casein, and Wesson salts were mixed together and ground in a ball mill for 24 hours. The remaining ingredients, excepting cholesterol and linseed oil, were dissolved in water and blended into the ground mixture using mortar and pestle. After mixing thoroughly, the diet was allowed to dry in shallow trays and ground again. The cholesterol and linseed oil were dissolved in chloroform and blended with the diet, using a mortar and pestle. After drying in shallow trays, the diet was reground and stored in amber bottles under refrigeration.

Rearing.—Recently-hatched nymphs from several emergence pans containing water as the only source of nourishment were combined and distributed randomly among the various diets. These were placed in gallon battery jars containing several layers of surgical gauze (to prevent nymphs from drowning in spilled water and to provide a surface for gaining a foot-hold when young nymphs accidentally turn on their dorsa), several masonite platforms (for resting areas), a shallow dish of water (containing a pad of cotton to prevent drowning), and a shallow dish of food. The dishes were ringed with adhesive tape to provide traction for the young nymphs and the jars were coated with a thin film of vaseline on the inside upper 2 inches and capped with a screen-covered embroidery hoop. Water was replenished as needed and food was changed twice weekly.

Determination of Diet Efficiency.—Unless specified, each diet was replicated once in each test using 100 to 200 insects per replicate. Weight, mortality, and maturation were recorded periodically, at which times adults were removed and the rearing jars were emptied of refuse. Survival was based on the population count of the first observations, since the initial mortality was variable and did not appear to bear any relation to the type of diet. This was probably a consequence of the handling involved in transferring the nymphs from the rearing containers at the outset of the experiment.

In all cases a standard diet consisting of Gaines Krunchons was included as a check on the performance of the synthetic diets.

RESULTS

Studies were made of the effects of dietary inositol on the growth and development of the American cockroach, *Periplaneta americana* (L). The data shown in table 1 and figure 1 are mean values of six experiments, each containing replicated diets and 100 to 200 insects per replicate.

During the first 50 days, growth and survival rates of the deficient and supplemented colonies were comparable. Shortly thereafter, however, there was a marked reduction in growth and a gradual increase in mortality, and after 270 days the insects on the deficient diet weighed 60% less than those receiving inositol and showed a mortality almost six times as high.

The inositol level for the initial studies was 2500 mg./kg.; comparison with standard dog pellet diet (which contains approximately 800 mg. of inositol per kg.) indicated that the concentration was excessive. Further experiments were conducted to determine the minimum quantity necessary for satisfactory growth, survival, and maturation, using levels of 100, 500, 1000, and 2500 mg./kg. Each diet was replicated once using 100 insects per replication. All diets were equally efficient (tables 2 and 3) and thus the critical level is below 100 mg./kg. Growth and development on the inositol-deficient diet

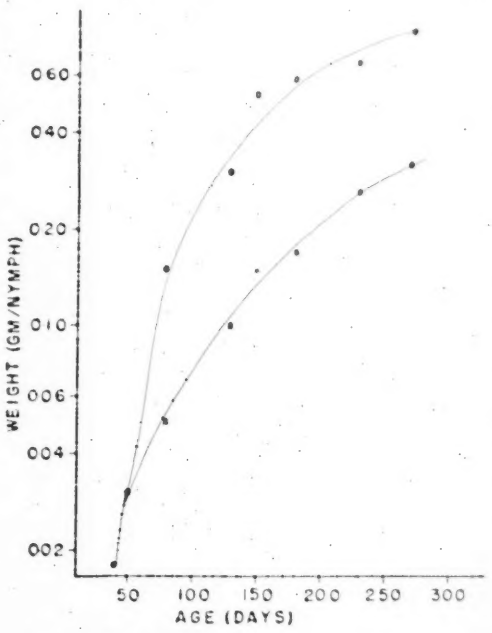

FIG. 1.—The effect of inositol on the growth of the American cockroach. (x=inositol-deficient diet; ⊙= diet containing adequate inositol).

was retarded markedly, as in earlier experiments. At 270 days cockroaches which were denied inositol weighed less than one-half as much as the controls and had four times the mortality. Only one individual attained maturity and as in previous experiments, the deficiency did not manifest itself during the first 50 days.

DISCUSSION

Generally speaking, inositol is not considered a dietary requirement for insects, since studies on a number of species have shown that they can be reared successfully on diets devoid of this com-

Table 1.—Effect of inositol on growth and survival of the American cockroach

Time on Diet	Inositol-deficient Diet		2500 mg. Inositol kg. diet	
	Wgt. ± Avg. Dev.	Survival ± Avg. Dev.	Wgt. ± Avg. Dev.	Survival ± Avg. Dev.
days	mg./nymph	%	mg./nymph	%
40	16±2		18±3	
50	32±5	97±2	30±2	100±0
80	50±5	81±4	150±13	98±2
130	100±11	70±8	300±18	97±2
150	151±10	53±7	519±32	94±4
180	172±19	45±10	581±29	90±7
230	190±16	39±9	648±41	87±8
270	323±28	25±7	820±27	87±8

Table 2.—The effect of varying dietary levels of inositol on the growth and survival of the American cockroach.

Time on Diet[a]	Weight ± Average Deviation					Survival ± Average Deviation				
	VA	VI^{0}	VI^{1000}	VI^{500}	VI^{100}	VA	VI^{0}	VI^{1000}	VI^{500}	VI^{100}
days	mg./nymph					%				
50	33±5	29±4	32±5	27±8	26±5					
100	150±7	68±3	145±7	138±6	153±3	97±2	84±2	95±3	91±2	96±1
150	690±25	149±17	626±16	590±26	651±13	92±4	67±3	88±1	80±1	86±3
180	750±18	173±43	656±59	686±19	738±55	92±8	48±2	88±1	80±0	86±2
230	773±62	242±52	673±8	664±12	770±3	92±9	33±1	88±2	77±3	84±3
270	756±12	363±58	777±3	786±66	835±5	90±7	25±4	88±2	77±3	84±3

[a]VA=Gaines Krunchons
VI^{0}=No inositol
VI^{1000}=1000 mg. inositol/kg. diet
VI^{500}=500 mg. inositol/kg. diet
VI^{100}=100 mg. inositol/kg. diet

Table 3.—The Effect of varying dietary levels of inositol on maturation of the American cockroach.

Diet[a]	Number Attaining Maturity[b]							
	150 days		180 days		230 days		270 days	
	Females	Males	Females	Males	Females	Males	Females	Males
	%	%	%	%	%	%	%	%
VA	10	0	26	5	50	26	52	36
VI^{2500}	0	0	13	3	28	21	33	30
VI^{1000}	1	1	20	17	33	39	38	48
VI^{500}	2	0	12	4	36	23	42	31
VI^{100}	2	1	15	15	34	37	34	48
VI^{0}	0	0	0	0	2	0	3	0

[a]Code designation for diets same as in Table 2.
[b]Expressed as accumulated percentage of survivors.

pound. Furthermore, it has never been demonstrated as a requirement for any insect species (Lipke and Fraenkel 1956), although several grew slightly better when it was included in the diet. If it can be assumed that insects utilize inositol, these species must synthesize it themselves or obtain it from symbionts.

A curious situation is presented in *Ptinus tectus*, which on inositol-free diets showed a slight growth reduction which was intensified by the simultaneous omission of para-amino benzoic acid (Fraenkel and Blewett 1943b). Since growth was affected only slightly on a PAB-free diet, it may be that the inositol requirement of that species was supplied by intestinal flora which required added PAB to synthesize the necessary quantity of inositol.

Apparently this is not the case with the American roach, for in the absence of inositol there is a marked reduction in growth and survival (tables 1 and 2; figure 1), and practically no maturation (table 3). Newly emerged nymphs placed on a deficient diet appeared to do well for the first 7 weeks. Probably there is sufficient inositol carried over from the embryo to satisfy the requirement during this initial period. Soon thereafter, however, the growth rate was affected so adversely that at 80 days the deficient individuals weighed only one-third as much as those receiving adequate inositol. The effect on growth persisted at or above this level for approximately 6 months or more. At age 270 days, the weight difference had narrowed somewhat, the deficient insects weighing 60% less than the controls. From the 50th day on there was a high mortality in the deficient colony and at 270 days only 25% had survived as compared to 87% in the colony receiving inositol.

The importance of inositol in the growth process is illustrated further in the data of table 3. At 270 days only 3% of the survivors on the deficient diet had attained maturity, whereas the average maturity in those colonies receiving inositol was 76%.

The critical concentration for inositol is below 100 mg./kg., since diets containing 2500, 1000, 500, and 100 mg./kg. were equally efficient in support of growth, survival, and maturation.

Generally speaking, the synthetic diet used in this study was slightly less efficient than Gaines Krunchons (dog food pellets), which contain sufficient inositol (800 mg./kg.) and are a standard rearing medium. The rate of maturation (table 3) was somewhat less rapid on the synthetic diet, which was true also in previous tests, the first adults always appearing in colonies receiving Krunchons. Survival and weight gain (table 2) were slightly better on the pellet diet; this is consistent with the results of other experiments, except for variations in the absolute values and in the magnitude of the differences from test to test. With respect to growth both the synthetic and Krunchon diets appeared superior to the dog biscuit and synthetic diets of Noland *et al.* (1949) and the raw potatoes and lean meat diet used by Gier (1947), for at 100 days weights for the American roach were 96 mg. (Noland) and 50 mg. (Gier) as compared to approximately 150 mg. on the diets used in this study.

The drop in average weight that sometimes occurs, e.g., in the VA group between 230 and 270 days (table 2), is not a true loss in weight but simply a lowering of the average weight as a result of removal of the mature individuals.

Although the synthetic diet compared favorably with the standard food with respect to growth, maturation, and survival, nothing is known concerning its effect on egg deposition, egg viability, and successive generations.

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OBITUARIES

Raymond Hill Beamer

1889–1957

Dr. Raymond Hill Beamer, 68, retired University of Kansas professor of entomology and curator of the Francis Huntington Snow Entomological Collections, died November 21, 1957 after a long illness. He was a skillful and enthusiastic collector of insects in all orders except the Lepidoptera and as a result the Francis Huntington Snow Entomological collections, which he served for so many years, are widely known to contain

"a gold mine of material" for specialists of all orders. Between 1914 and 1954 he led 29 collecting parties on extended trips and made 14 other trips on special assignments.

In all these years as Professor of Systematic Entomology he taught Insect Taxonomy and inspired and meticulously guided many research students in problems on the Homoptera and was a productive scholar himself, publishing 107 papers in which he described 563 new species and 9 new genera.

Although Dr. Beamer's interests as a collector and biologist were quite diversified, his taxonomic work was limited almost entirely to the Auchenorrhynchous Homoptera. His early work on the biology of cicadas resulted in an extensive and enduring knowledge of the taxonomy of those interesting insects. He turned next to the genus *Erythroneura* and his elucidation of the seemingly innumerable species of this prolific genus is an outstanding example of patient and meticulous study. From *Erythroneura* he turned to the Deltocephaline leafhoppers and other grass-inhabiting groups of Cicadellidae. Later he worked extensively in the Delphacidae, contributing greatly to the understanding of the North American fauna in all groups studied.

As curator of the entomological collections, during the school year he trained many students in museum techniques and during summer vacations took advanced major students into the field to collect for the museum and to learn how to conduct entomological surveys.

His colleagues and former students at the University of Kansas are dedicating the April 1958 number of the Journal of the Kansas Entomological Society as a memorial to Dr. Raymond Hill Beamer. In it will be found an extended biography, his bibliography, a record of his field trips and some of his accomplishments and honors.

H. B. Hungerford
P. W. Oman

Teiso Esaki

1899–1957

Dr. Teiso Esaki, dean of Japanese entomologists, was born in Tokyo, July 15, 1899. He was brought up in Osaka, where he attended primary and middle schools. He attended higher school at Kagoshima, then studied in the Zoological Department, Faculty of Science, Tokyo Imperial University, from 1920 to 1923. He took his Doctor of Science degree at the latter department in 1930.

Dr. Esaki is widely known as an active and broad entomologist. He authored many works on various aspects of Japanese entomology, including history, texts, taxonomy, and some of the faunal works, splendidly illustrated with colored photographs, for which Japan

is so noted. He is also internationally known for his work on Heteroptera of various parts of the world, for his work on Micronesian insects, and for his wide travels and contacts.

In 1923 Esaki was appointed Assistant Professor of Entomology in the College of Agriculture, Kyushu Imperial University, at Fukuoka. In February, 1924, he went abroad for a stay of more than 4½ years. He spent most of this time in Germany, Hungary, England, Italy, and France, but visited the United States, including Hawaii, for 2 months on his way back to Japan. He was a good linguist and quickly learned to speak German, English, Hungarian, Italian, French, and Esperanto. In Budapest he worked on Hemiptera under the great Dr. G. Horváth, and published a number of papers in German and Hungarian as well as in English.

Esaki met Charolotte Johanna Hermine Witte on the Danube in 1924, again in Geneva, and at her home in Herford, Germany, in 1927. They were married in Herford in May, 1928, and reached Japan the following August. Dr. Esaki is survived by Charlotte and four children: three daughters, Haruko-Lies (Mrs. Suzkui), Luli, and Erica (Eriko), and one son, Peter Tetichi, the youngest, who is not yet through college.

In 1930 Esaki became Professor of Entomology at Kyushu University, a position he held the rest of his life. In 1932 he made a collecting trip to Taiwan, and in 1934 one to the Ryukyu Islands, Taiwan, and Korea. In January, 1936, he started his first trip to Micronesia, where he visited Saipan, Palau, and Yap. Late in 1936 he was appointed Director of the Hikosan Biological Laboratory of Kyushu University. His second Micronesian trip, in 1937, to Saipan, Truk, Ponape, Jaluit, and Kusaie, was followed by a third in 1939, when Saipan, Truk, Ponape, Palau, and Yap were revisited. In 1940 Professor Esaki sent Dr. K. Yasumatsu and a student, Mr. S. Yoshimura, to Saipan, Pagan, and Truk for further field work. As a result of this considerable field work in Micronesia, material was submitted to many specialists for study. The reports were published in various journals, but each bore a footnote subtitle, "Results of Professor T. Esaki's Micronesian Expeditions (1936–1940), No. . . . ". Eighty-two of these reports (not all on insects) were published before the commencement of the "Insects of Micronesia" series by Bishop Museum. Dr. Esaki very kindly turned over his unstudied Micronesian material to Bishop Museum, and articles in the "Insects of Micronesia" series which include some of his material continue to bear the same footnote subtitle.

In 1939 Professor Esaki also made a trip to China, visiting Shanghai, Nanking, and elsewhere. In 1940 he went to Manchuria. In 1941–42 he visited Indochina, Malaya, and Taiwan on a 3-month trip related to basic research in zoology. In 1945 he was appointed to the Council of the Tropical Institute of Agriculture and Forestry. In 1946 he was appointed Councilor of Kyushu University. In 1947 he was attached to the Medical Specialist Department of the University. In 1949 he was appointed Dean of the College of Agriculture, which position he held for 2 years. In 1951 he was appointed Commissioner of both Botany and Zoology committees of the Japanese National Research Council.

In 1950 Dr. Esaki was elected a member of the International Commission on Zoological Nomenclature. In 1953 he attended the Nomenclature Colloquium and the XIV International Congress of Zoology at Copenhagen. This was on a 5-month trip during which he visited museums in Denmark, Germany, Great Britian, France, and Italy.

In 1955 Dr. Esaki was appointed Dean of the General Education Department, the equivalent of the undergraduate college, of Kyushu University. This deanship he also held for 2 years, up until a few months before his death. In 1956 he developed a tumor on his neck. This was removed, and proved to be cancerous. He continued his work after this, and another operation, for nearly 2 years.

In October, 1957, as President of the Entomological Society of Japan, Professor Esaki officiated at the 40th anniversary of the Society in Tokyo, during which the Emperor visited the exhibition connected with the meetings. A photograph published in the magazine "Shin Konchû" (New Entomology) showed him explaining exhibits to the Emperor. Following his return to Fukuoka after these meetings, his condition worsened rapidly and in 2 months he passed away. Both Dr. Usinger and I planned to visit Professor Esaki on our return to the United States from the Ninth Pacific Science Congress in Bangkok. Dr. Usinger reached Fukuoka a week before Esaki's death, but Dr. Esaki was then too ill to see him; and I arrived 2 days after Professor Esaki's death, and called on the family.

J. Linsley Gressitt

STUDIES ON THE COMPARATIVE ETHOLOGY OF DIGGER WASPS OF THE GENUS BEMBIX, by Howard E. Evans. Cornell Studies in Entomology. Comstock Publishing Associates, Cornell University Press, Ithaca, N. Y. viii+248 pp., 52 figs. $4.75. Paperbound.

Dr. Evans introduces us to the wasps whose habits have occupied his attention for the past 5 years by saying, "The genus *Bembix* includes some of the most familiar digger wasps. . . . They nest in the ground, more or less gregariously and provision their nests with flies. They have been popular with naturalists ever since the early observations of Linnaeus, 1745, in Sweden and John Bartram, 1763, in Pennsylvania." A long series of investigators has studied these interesting aculeates. Linnaeus and Bartram were followed by such students as Fabre in Southern France, Hartman in Texas, Rau in Missouri, the Peckhams in Wisconsin, and Parker in California. The literature on *Bembix* was summarized in 1945 by the Danish entomologist Nielsen. The studies thus reviewed were predominantly observational investigations on single species.

Evans set out to make a comparative study of the habits of 13 species. He studied these wasps in the field, in Kansas, California, and Florida. For each species he determined the feeding and mating habits of the adults, the locating and constructing of the nest, its provisioning, the development of the young, and the parasites and predators with which the wasps had to contend.

It became clear during the course of these studies that there are distinct and consistent differences in habits among these species of *Bembix*. The adults are morphologically very much alike, but their habits are quite diverse. Evans devotes the last 60 pages of his book to an analysis of these differences, and he concludes with a discussion of the probable evolutionary sequence of the behavior patterns. His findings do not show that there is an agreement between developing behavior patterns and taxonomic categories below the species level. He states, "On present evidence I am inclined to believe that subspecies are merely regional variants in color or in other superficial characters and by no means 'species in the making'".

B. D. Burks

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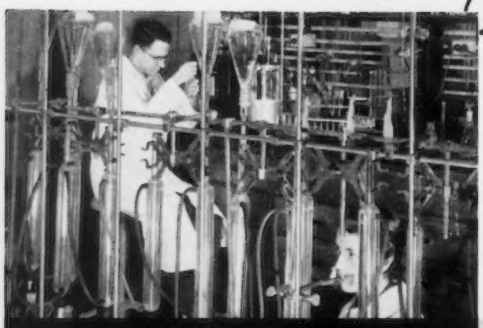

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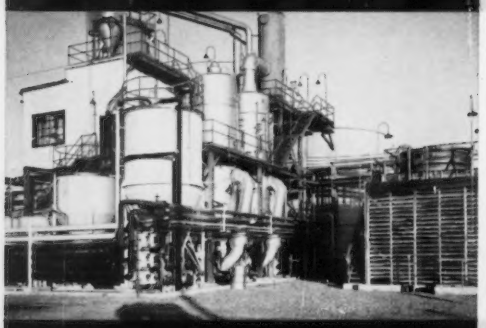

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